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# HEREDITAS



# PRIMARY AND SECONDARY ASSOCIATION IN TARAXACUM

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## INTRODUCTION.

BY extensive studies of the early stages of meiosis the English school of cytology (DARLINGTON and his co-workers) has succeeded in presenting a clear and uniform picture of the process of chromosome pairing and the causes of that »variety of mitosis» which meiosis constitutes (DARLINGTON, 1932). The most important points of this fundamental theoretical structure are the following:

During the leptotene stage the chromosome threads are undivided, they are paired at zygotene, split lengthwise at pachytene, and by exchange of segments in pachytene — diplotene the four chromatids form a bivalent, the chromatids of which are separated two and two at anaphase. The ultimate cause of the pairing of the chromosomes is the precocity of the meiotic prophase, which results in division commencing before the individual chromosomes have divided and therefore the attraction is between two chromosomes instead of between two chromatids. Hence, all true bivalents in the metaphase of meiosis are derived from an exchange of segments (primary association) and only these bring about a regular distribution of the chromosomes at the two anaphase poles.

Chromosome attraction can also occur, however, in later stages — occasionally at mitosis — but owing to the fact that chiasma formation does not take place there the chromosomes are not connected with one another (LAWRENCE, 1931, and DARLINGTON, 1932).

These facts, derived from cytological and genetical observations of sexual biotypes, can also be subjected to analysis with respect to the course of meiosis in parthenogenetic apomictic plants. For in these groups there exists in *E. M. C.* a connection in the first place between a »mitotising» of meiosis, secondly an omission at prophase of the formation of pure gemini and thirdly a »general diffuse» attraction in later stages between certain chromosomes (false gemini formation, »pure» secondary association).

have cursorily dealt with this condition in another paper (GUSTAFSSON, 1934), when I endeavoured to show that the origin of forms in complete apomictic species can be explained by a non-division of »gemini» chromatids in the so-called pseudo-homotypic phase, or, as DARLINGTON asserts (1932, p. 473), by crossing-over, after provided that bivalents are sometimes formed by means of centromere exchange at prophase. I also showed in the above-mentioned paper that plant-geographical and systematical observations are explained only by means of this process of pseudo-mutation in the pro-sac mother cell.

A detailed analysis of these conditions will be given in a future paper which I have ultimately in view, viz. a classification of apomictic amphipomictic species within the phanerogam system into systematic and phylogenetic groups.

The apomictic plants examined in the following account are *T. racemum Nordstedtii* DT. ( $2n=48$ ), an auto-hexaploid form of uncertain classification, *T. Kalbfussii* HAND. MAZZ. ( $2n=24$ ), 1930: 632, *T. alpinum* (HPPE) KOCH coll. ( $\times$  *Pacheri* SCH.-BIP.?) ( $2n=24$ ), both belonging to the *T. alpinum* complex, 1930: 635, *T. ceratophorum* EB. from the Alps ( $2n=32$ ), 1930: 712, probably *T. lactucaceum* ( $2n=32$ ), 1930: 671, probably *T. simulum* BRENN., ( $2n=32$ ), the last-mentioned also belonging to *Ceratophora*, an indefinite form of *Erythrospermum*, 1930: 287 ( $2n=24$ ), also an indefinite form of *Galium*, 1930: 221 ( $2n=24$ ). At least some of the above species, such as *T. Kalbfussii*, *T. alpinum* ( $\times$  *Pacheri*?), 1930: 287 and 1930: 221, with a certain degree of probability allopolyploids. All specimens have been fixed in Navashin's ordinary formalin — acetic acid — chromic acid solution with a few minutes' preparatory fixation in Carnoy with chloroform. The sections were cut 10—20  $\mu$  in thickness and stained with gentian violet.

## FORMATION OF GEMINI IN P. M. C.

*T. Nordstedtii* DT. (v. also GUSTAFSSON, 1934, p. 281). Figs. 1—9. — This biotype occasionally forms pollen sacs with divisions, but P. M. C. never reach beyond the four nuclei stage, degenerating instead shortly afterwards.

Fig. 1 shows a complete metaphase, seen from the side. A fairly positive analysis of the association was possible in spite of the large number. In contradistinction to all triploid biotypes it exhibits com-

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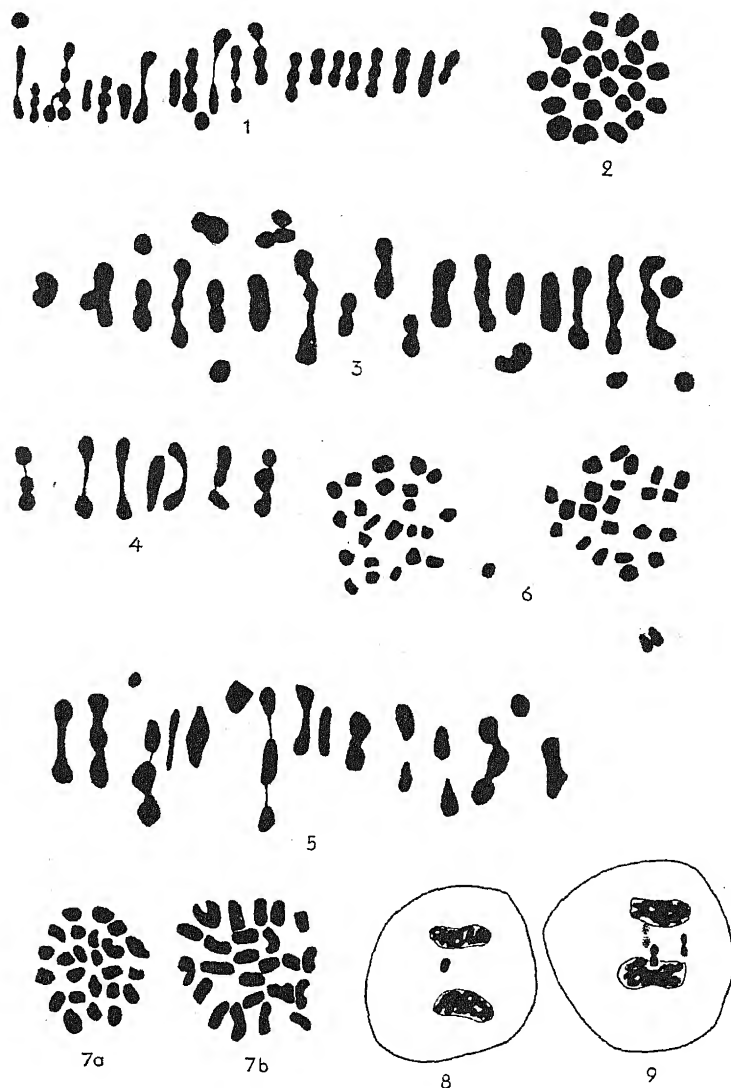
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plete pairing with chiasmata that are to a great extent terminalised at metaphase. One evident quinquevalent, one trivalent, nineteen bivalents and two univalents could be observed. Fig. 3 shows an unfor-



Figs. 1—9. *T. Nordstedtii*. P. M. C. — 1 and 3. Heterotypic metaphase side view. — 2. Heterotypic metaphase polar view. — 4. Trivalents and bivalents from different heterotypic metaphases. — 5. Incomplete heterotypic metaphase. — 6. Heterotypic anaphase. — 7a and 7b. Heterotypic metaphases. — 8. Telophase with one lagging chrom. — 9. Telophase with one lagging chrom. — Figs. 1—7 2600 X, Figs. 8—9 1600 X.

unately obliquely cut metaphase, in which the bivalents do not lie entirely in one plane. It probably shows to the extreme left a trivalent with a »triple chiasma», and farthest to the right a »linear trivalent». The large trivalent-like configuration in the centre is probably only a bivalent. An analysis will thus show  $2_{III} + 18_{II} + 6_I$ . Fig. 5 represents an incomplete metaphase with two trivalents and two univalents; Fig. 4 three trivalents and a few bivalents from different plates, while Fig. 2 shows a metaphase seen from above: 24 elements can be observed but I dare not express any definite opinion as to whether they are exclusively bivalents or solitary trivalents and univalents.

The separation at metaphase—anaphase proceeds as a rule fairly regularly. The polyvalent formation of course involves an uneven distribution of the chromosomes, and now and again lagging chromosomes, sometimes divided, are noticed to be merged into the anaphase plate or to form small nuclei. Fig. 8 shows a telophase with an undivided lagging chromosome, and Fig. 9 three divided lagging chromosomes. Fig. 6 represents a heterotypic anaphase with  $24 + 22$  and two more chromosomes lying outside them, and Figs. 7 *a* and 7 *b* show homotypic plates from two P. M. C. with 24 chromosomes in each.

This intense production of gemini, which shows itself to be constant in different P. M. C., is the reason why, as far as could be ascertained, no »dyads» are ever formed and seldom any »polyads» with the exception of a few solitary »pentads» — as mentioned above P. M. C. degenerate after the second division. The somewhat varying univalent formation (Table 1) is due, according to the chiasmotype theory, to the fact that chiasmata are not formed between all chromosomes owing to the competition between the homologue chromosomes.

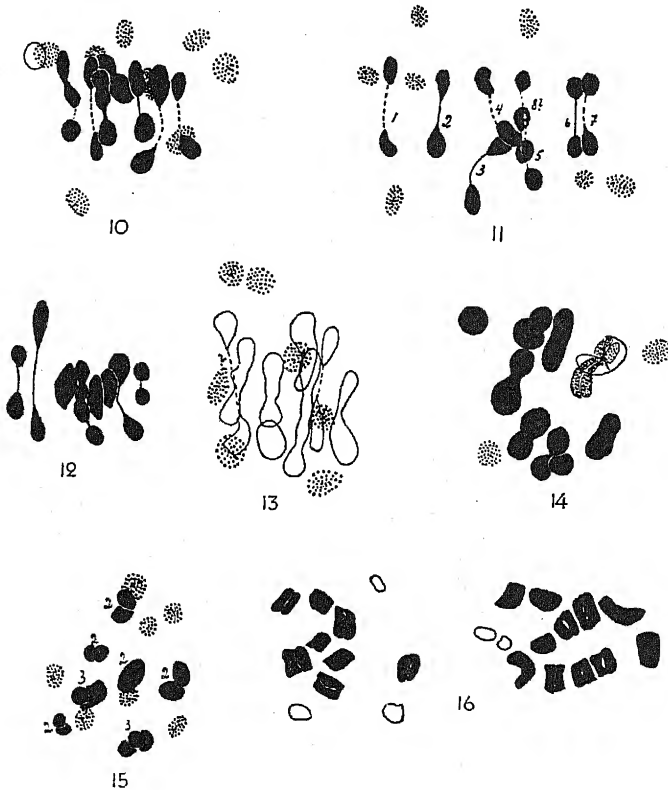
TABLE 1. *Univalent Formation in T. Nordstedtii* DT.

Number of univalents	0	1	2	3	4	5	6	7	8
Number of P. M. C.	21	16	13	5	8	5	—	—	1=69

The Table, which is based on calculations from metaphases in side view, shows that the number of plates in which *all* elements are in some way or other associated amounts to 30 % and the number of plates in which more than two univalents appear amounts to 27 % of all cases.

*T. Kalbfussii* HAND. MAZZ. Figs. 10—16. — This appears to agree with the so-called *Drosera* sch.

hybrid set  $8_{II} + 8_p$ , but with this difference that trivalents are formed occasionally. ROSENBERG (1909) and TÄCKHOLM (1922), who have made a close study of and outlined the theory for this scheme, did not, it is true, observe any trivalents or polyvalents in their respective plants, but it is nevertheless probable that such associations can occur, even if only occasionally. Here they occur, however, rather commonly.



Figs. 10—16. *T. Kalbfussii*. P. M. C. — 10—15. Heterotyp. metaphases. — 16. Heterotyp. anaphase. — 2600  $\times$ .

Fig. 10 shows a metaphase in side view with (6—)7(—8) bivalents. Furthest to the left is seen a configuration which is probably a trivalent: if this interpretation is correct the plate contains  $1_{III} + 6_{II} - 7_{II} + 9_I - 8_p$ . As in other plates, the terminal chiasmata are plainly discernible here. Fig. 11 shows another metaphase with at least 7, at most 8, gemini, the bivalent labelled 8? lay so close to Nos. 3, 4 and 5 that it was not possible to decide with certainty whether there was any

the attachment present, for it may happen, even if rarely, that some of the unpaired elements do not lie outside the bivalents but dispersed among them. Seven univalents lay clearly apart. There was no sure evidence of the occurrence of any trivalent. Fig. 12 shows the paired elements from another P. M. C. Here one trivalent and seven bivalents were observed. Fig. 13 represents 1—2 trivalents and 4—6 bivalents. Whether the large formation in the centre is a combination of 3 or 2 is difficult to decide, its unusual size undoubtedly indicates the former. On the extreme right is seen a bivalent which is rather striking owing to evident difference in size between the two parts. As such a geminus could not be regularly discovered in other P. M. C. it is probably nothing but an incidental deviation (compare however Fig. 14). Gemini did not appear to lie exactly on the plate, which was due to the pollen-sac having been cut obliquely. Fig. 14, although not complete, shows very beautifully one trivalent and seven bivalents, Fig. 15 1—2<sub>III</sub> + 6—5<sub>II</sub>.

The further course of meiosis does not present any features of particular interest. In Fig. 16 are seen two anaphase plates, the distribution of the chromosomes being 11 + 13. The longitudinal division is plainly visible and some of the chromosomes already possess the homotypic appearance. No restitution nuclei were ever observed, as was also the case in *T. Nordstedtii*. The formation of such restitution nuclei and the occurrence of a low number of gemini are correlated (v. GUSTAFSSON, 1933, p. 532). Pollen is produced but varies in size: in the »tetrads» quite a number of small nuclei occur, as shown in Table 2, no doubt due to certain lagging univalents.

TABLE 2. *Formation of Tetrads in T. Kalbfussii.*

Number of nuclei after							
homotypic division	2	3	4	5	6	7	8
Number of P. M. C.	—	1?	71	15	6	—	— = 95

It should be observed that diakinesis in both the preceding species and this one have of course been studied but no definite conclusion could be arrived at. It is however sure that a large number of bivalents were to be observed at this stage in *T. Kalbfussii*.

These two apomictic plants are therefore characterised by slightly varying formation of bivalents, the only change being in the number of tri(-poly)valents, as is to be expected in accordance with the chiasma-type theory. It can thus be assumed that in both cases the highest

number of associations observed also indicates the maximal number due to the chromosome homology.

For the sake of a comparison with these two biotypes having a constant number of bivalents I shall describe meiosis in an apomictic plant, 1930: 632, obtained from Dr. HANDEL MAZZETTI under the name of *T. alpinum* ( $\times$  *Pacheri*?). The diploid number is  $2n = 24$ .

In 1917 and 1927 ROSENBERG described the so-called *Hieracium boreale* type, that is, in meiosis in forms belonging to this type there occur a varying number of gemini (mostly only a few), frequently none at all (semi-heterotypic metaphase). A very interesting point to note is the different frequencies of the gemini in different ages (ROSENBERG, 1927, p. 318). This proves that the semi-heterotypic division is not necessarily determined by deficient chromosome homology, rather, the genes which regulate the course of meiosis and pairing in P. M. C., the presence or absence of which is entirely without any importance in these totally apomictic plants, may have in the course of time been lost through a series of eu-mutations or pseudo-mutations (GUSTAFSSON, 1932 b, p. 112).

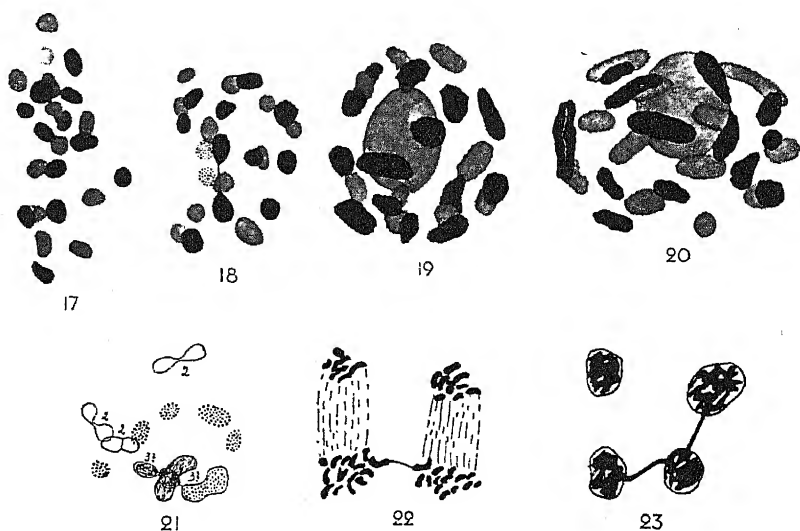
*T. alpinum* ( $\times$  *Pacheri*?). Figs. 17—23. — Fig. 17 shows a semi-heterotypic division, Fig. 18 a metaphase with one geminus, while Figs. 19 and 20 show two diakinesis with 0 and 1 bivalent respectively. Already at this rather early diakinetic stage complete terminalisation can be seen, a phenomenon which is always more pronounced in metaphases with a small or varying number of gemini than in metaphases with extensive or complete pairing, where one or more interstitial chiasmata can often be observed. But, as pointed out above, this *need* not by any means be connected with a low degree of chromosome homology, which determines a low frequency of chiasmata, for it has been possible to ascertain up to 8 gemini even in forms with predominant semi-heterotypic division, or that in E. M. C. the formation of »pseudo-gemini» in triploid biotypes can amount to this number (GUSTAFSSON, 1934). Such a P. M. C. with a large number of bivalents is shown in Fig. 21, in which there probably occur two trivalents and three bivalents, at any rate at least five gemini. It should be emphasized however that secondary association is not entirely out of the question and it may therefore only be a case of »pseudo-gemini», in the same manner as in E. M. C.

The succeeding stages do not present anything of special interest. Associated with the random distribution of the chromosomes at the two

poles is the formation of restitution nuclei. Of 54 P. M. C. in homotypic metaphase 21 cases (i. e. 39 %) showed one plate, 32 cases (59 %) two plates and 1 case (2 %) three plates. Table 3 shows the chromosome distribution, where no restitution nuclei have been formed.

TABLE 3. *Chromosome Distribution in 1930: 632.*

Chromosomes in homotypic metaphase	12 + 12	13 + 11	14 + 10	15 + 9	16 + 8	17 + 7	
Number of cases	3	6	7	4	4	1	= 25



Figs. 17—23. *T. alpinum* ( $\times$  *Pacheri*?). P. M. C. — 17. Semi-heterotyp. metaphase. — 18. Heterotyp. metaphase with one bivalent. — 19. Semi-heterotyp. diakinesis. — 20. — Diakinesis with one bivalent. — 21. Incomplete heterotyp. metaphase. — 22. Homotypic anaphase. — 23. The formation of triploid pollen grains (?). — 2600  $\times$ .

Theoretically of course the peak of the distribution curve should be expected to be at  $12 + 12$ , but a tendency towards other numbers of distribution is evident. Is this perhaps connected with the occurrence of secondary association, which brings about a common movement of chromosomes?

Fig. 22 shows a homotypic anaphase, in which a chromatin thread connects two chromatids from the two sister plates. Such bridges can of course give rise to the formation of restitution nuclei even in the homotypic phase. Such a chromatin connection between three tetrad

nuclei is seen in Fig. 23. Here there should be formed a triploid pollen grain.

As mentioned above, several things indicated the occurrence of secondary association in P. M. C. with bivalents but no definite conclusion was possible. The same is true in studies of biotypes with *exclusively* semi-heterotypic division. Here I sometimes noticed that the univalents were occasionally situated in pairs close to one another even if they were in different planes. Further studies must throw light on this problem, which may be of particular importance.

Before beginning to study the development of E. M. C. I had succeeded in showing in P. M. C. the gradual increase in the number of »gemi» from diakinesis to metakinesis and metaphase in two biotypes (Table 4).

TABLE 4. *Number of Gemini in Different Stages.*

	In diakinesis	Average	In prometa- phase	Average	In meta- phase	Average
<i>T. lance- olatum</i>	2 to 3, 2, 2, 3, 3, 3, 3, 2, 3, 2 to 3, 1?	2,5	5, 3, 3, 3	3,5	5 to 6, 4 to 5 5 to 6, 5, 1, 2, 4 to 5, 2 to 3, 4—5—6	3,9
1929:5	1		2, 3		7, 6—7, 6 8 to 9	

This increase is therefore quite apparent in spite of the smallness of the material. Difficulties of fixation in the diakinetic stages or the rapid passage of prophase to anaphase in many biotypes make statistical observations, however, rather uncertain. The divisions of E. M. C. show that this is nothing but the occurrence of secondary association. It should be remarked, however, that »pseudo-gemi» in these two forms, contrary to what one would expect with secondary association, seem to arrange themselves in the heterotypic plate. But P. M. C. exhibit so many disturbances at metaphase (an account of which will be given in a future paper on the formation of restitution nuclei), sometimes owing to the formation of membrane about the separate gemini, that this objection is perhaps unjustified.

#### OCURRENCE OF GEMINI IN E. M. C. AT DIAKINESIS.

The development of the embryo-sac mother cell proceeds along the following lines: By suppression of the attracting forces at prophase no

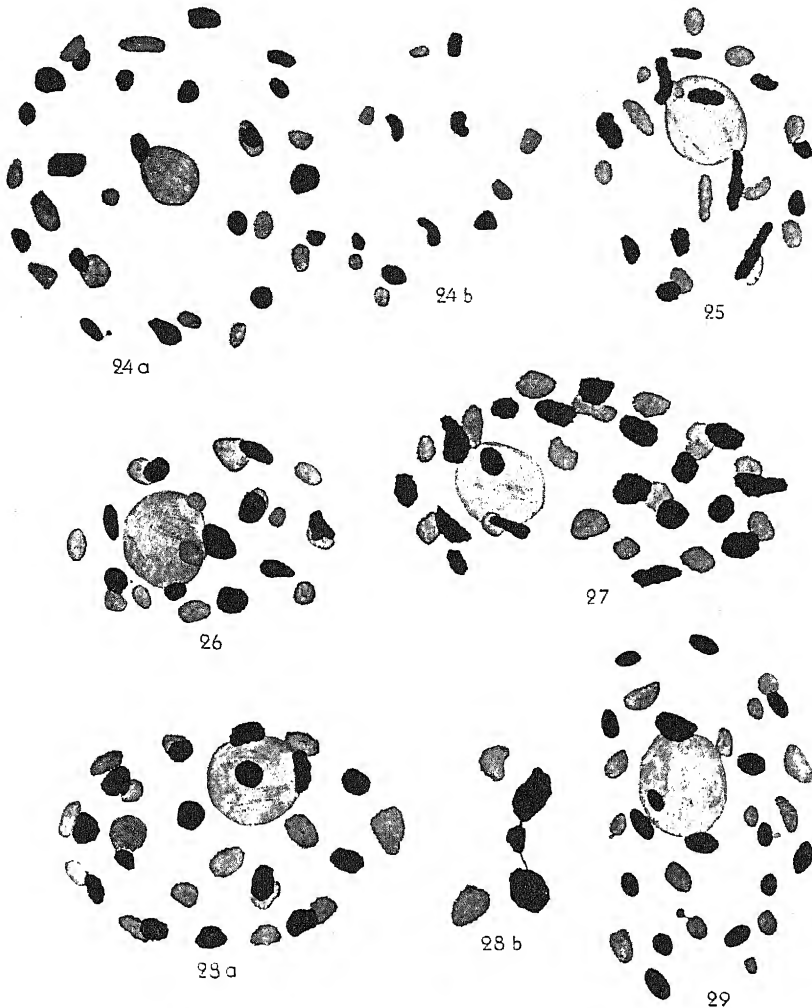


pairing takes place and consequently there is no exchange of segments between the homologous chromosomes; for this reason no primary associations, or at any rate but few, are met with in the diakinetik stage. However, associations can be observed at metaphase. The method of origin of these associations must be as follows: By incidental proximity or »diffuse attraction» at the final stage of diakinesis more or less homologous chromosomes touch and form »pseudo-gemini», which in many cases do not differ in appearance from eu-gemini in P. M. C. In the *Antennaria* type such a phenomenon has not yet been observed. Here the metaphase chromosomes in all sure cases form a pseudo-homotypic plate with highly contracted univalents, which divide lengthwise at the homotypic metaphase. In both sure instances in the *Taraxacum* type (*Taraxacum*, *Chondrilla*) the chromosomes are similarly contracted, but in addition to the process occurring in *Antennaria* and others the chromosomes (owing to the stretching of the spindle? See p. 20) may be carried towards the two poles so that incipient anaphases are formed. A membrane develops around these chromosomes so that nuclei with the somatic number are obtained. Hence, in *Taraxacum* there occur a homotypic and a pseudo-homotypic division, whereas in *Antennaria* only the latter occurs. In this way the »diploid» embryo-sacs originate (GUSTAFSSON, 1934).

According to this line of reasoning, which should simplify the problem considerably, the only difference between the *Taraxacum* and the *Antennaria* schemes (with the exception of the two different phases in *Taraxacum*) is that in the former only one somatic macrospore participates in the formation of the embryo-sac while the other dies. In the latter case, on the other hand, no wall is built between the daughter-cells and both contribute in the development of the embryo-sac. The two types thus correspond to the normal type and the *Lilium* type in sexual species, although the number of steps from E. M. C. to a complete embryo-sac is reduced by one. Thus, they are *not* homologous with the *Scilla* and *Lilium* types.

In the paper mentioned above the method of the formation of pseudo-gemini was dealt with quite cursorily, in none of the forms discussed was the formation of pollen examined; in fact one of them, *T. dissimile* Dr., does not develop any P. M. C. which undergo meiosis. — Here then the first step is to examine the number of primary associations in diakinesis. Figs. 24—39 illustrate this stage in different forms. In their homogeneity they do not present any noteworthy feature, many more such illustrations could have been submitted if

necessary. Irrespective of the chromosome number ( $2n = 24, 32, 48$ ) all diakineses show only univalents. Only 7 cases, which are of interest

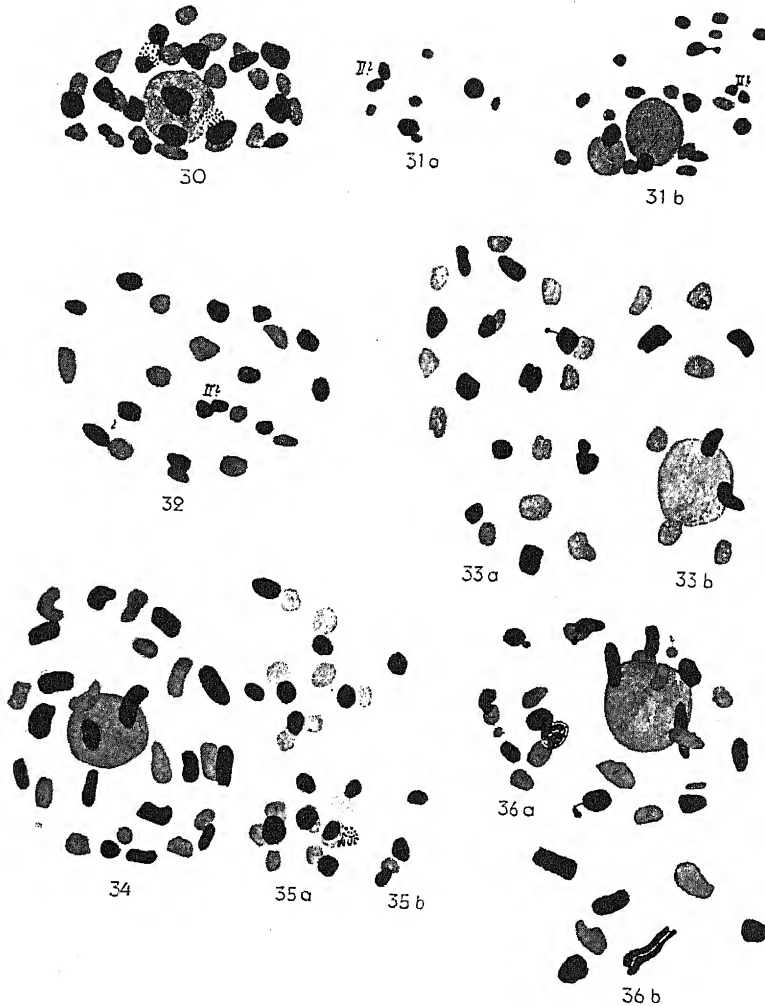


Figs. 24—29. E. M. C. Diakinesis stages. — 24. *T. Nordstedtii*. — 25 and 26. *T. Kalbfussii*. — 27 and 29. 1930:635. — 28. 1930:712. Here one terminal association. — 2600  $\times$ .

because they exhibit primary associations more or less apparently, will be subjected to closer analysis.

Figs. 24 *a* and *b*, showing an almost complete diakinesis in *T. Nordstedtii*, are very interesting; 47 unpaired chromosomes can be counted in

the two sections in spite of the complete pairing in P. M. C. and in spite of the probable autopoloid origin of this apomictic plant. They thus



Figs. 30—34 and 36. E. M. C. Diakinesis stages. — 30—32 and 36. 1930: 635. — 33—34. 1930: 712. — Fig. 35. E. M. C. Semi-heterotyp. metaphase. 1930: 712. — In 31, 32, 36 a false gemini. — 2600 X.

prove that not even a spontaneous reduplication is capable of altering the mechanism of pairing (v. also p. 28). Figs. 25 and 26 show two diakinesis in *T. Kalbfussii* with completely unpaired elements in spite of the constant number of gemini in P. M. C. Figs. 27, 29—32, 36 show

the same stage in 1930: 635 (*T. ceratophorum* from the Alps,  $2n = 32$ ). The formation of trabant-like segments as shown in Figs. 29, 31 and 33, which is often the case in P. M. C., could be seen occasionally. Figs. 33 and 34 represent two beautiful diakinetik stages in 1930: 712, probably *T. lactucaceum* Dt. The frequently plainly extended form of the chromosomes will be noticed, while those in Figs. 35 *a* and *b*, showing semi-heterotypic metaphase (unpaired chromosomes!), are more contracted.

Figs. 28, 31, 36 *a*, 37 and 38 show those cases in which more or less plausible formation of gemini could be observed. It must be very strongly emphasized — and this whatever their interpretation may be — that this postulated bivalent formation is an extremely rare occurrence at diakinesis, and of the cases enumerated here only one or two at most can be taken as evidence of a real primary association with chiasma formation and an exchange of segments. *In none of the E. M. C. in which diakinesis had reached its climax, and so having repulsion between the chromosomes most intense, could the slightest trace of gemini formation be discovered.* The nuclei most easily interpreted are shown in Figs. 37 and 38, although the latter, along with that of Fig. 28, was at first taken to be definite evidence of a primary association during diakinesis. In Figs. 37 *a* and *b* are seen two chromosomes furnished with appendages, the nature of which I am very uncertain about. They may perhaps be fragments or translocations. However in the following metaphase these appendages were never observed, 24 rounded (-square) chromosomes always being seen. Neither can this form be a »trisomic or tetrasomic» tetraploid. I have on a previous occasion described its chromosome number from root-tips (1932 a, p. 48) and found it to be  $2n = 24$ . While these appendages in Fig. 37 are in intimate contact with the »main chromosomes», in Fig. 38 *a* they are only connected to them by means of a thin chromatin thread. In the next section I discovered the three chromosomes shown in Fig. 38 *b*. There is no possibility of a mistake having been made. There is therefore no question here of any bivalent formation, the long chromatin thread is probably nothing but an unusually pronounced constriction (trabants are not so seldom observed either!) or the connecting link between a translocation and the principal chromosome (cf. however what has been said above with regard to the appearance of the metaphase chromosomes).

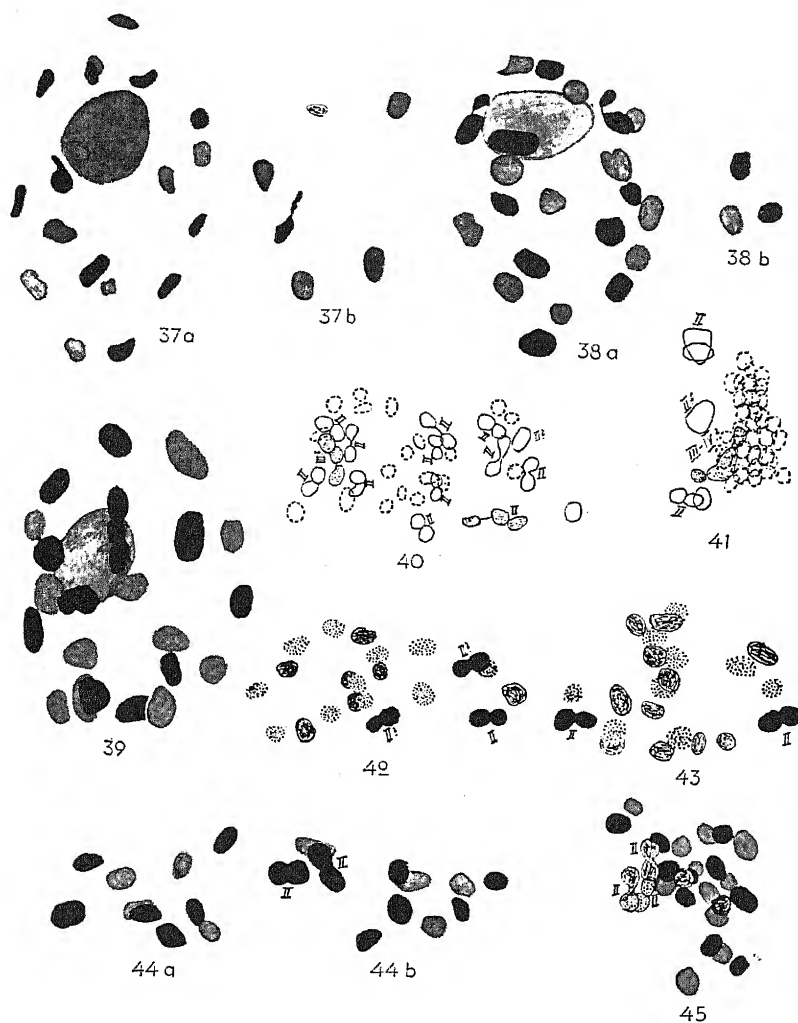
Again, in Figs. 31, 32 and 36 the occurrence of primary association is not definite, although there is an evident association present. In

36 *a* the two chromosomes lie close to one another but in a somewhat different plane; in Figs. 31 *a* and *b* they are in the same plane but clearly separated (most pronounced in *b*) while in Fig. 32 the two chromosomes (labelled II?) lie close together and are located in the same plane but even here it is probably only a question of a loose association. Furthest to the left in the same figure is seen a clear case of loose association, the two chromosomes are lying close together in different planes.

Fig. 39 will be found of great importance for the further development of our argument. To the left of the nucleolus the picture is schematic, it was in reality not so clear. In the upper part of the right half of the nucleolus there appear three chromosomes lying like a trivalent. However, I am convinced that there does not exist any primary association between them, for on focussing they were seen to be clearly separated from one another and not in any way fused. The attraction between more or less homologous chromosomes had in this case overcome the repulsion or the repulsion at this moment was not at its maximum strength. Hence, here, too, there occurred a formation of »pseudo-gemini».

There still remains Fig. 28. Here a chromatin thread association exists already at diakinesis; primary association possibly resulting from terminal affinity is in all probability present. However, even in this case the »bivalent» is not quite plain, one sees in the centre a sharply defined body of a considerably smaller size than the two bodies at the side. The chromosome number is  $2n = 32$ . In Fig. 28 *a* are seen 28 unpaired chromosomes while Fig. 28 *b* shows two univalents in addition to the trivalent-like formation. We have here, then, a bivalent; the central portion is nearer one of the bodies than the other, probably it is separated only by means of a very pronounced constriction, but it may be nothing but a fragment. Has this bivalent then arisen as the result of a chiasma which has already become terminalised (note however that the chromatin thread, apparently or really, does not go to the point of the lower chromosomes!)? DARLINGTON (1932, p. 332) has clearly interpreted the occurrence of a double affinity in the end particles of the chromatids, a terminal and a lateral, and on p. 333 he says: »Terminal affinity is exerted as a rule only when one lateral association is displaced by another in terminalisation. But if terminal affinity develops after diplotene the possibility arises of its being a secondary cause of pairing at diakinesis or metaphase». This assumption of a terminal affinity helps to explain the formation of pseudo-

gemini to be described below and will therefore be more probable even in this particular case. Bearing in mind also the enormous difficulties that a side-by-side pairing has to contend with, so that not even the



Figs. 37—39. E. M. C. Diakinesis stages. — 37 and 38. 1930: 221. — 39. 1930: 287.  
Figs. 40—45. E. M. C. Heterotypic metaphases. — 40 and 41. *T. Nordstedtii*. —  
42 and 43. *T. Kalbfussii*. — 44. *T. alpinum* (× *Pacheri*?). — 45. 1930: 635. —  
2600 ×.

chromosomes in the probably auto-hexaploid *T. Nordstedtii* are capable of forming bivalents or that the embryo-sac mother cell, reproduced in Fig. 55, which has arisen by a somatic doubling of the chromosome

number and which therefore certainly contains at least two completely homologous chromosomes of the same type, does not either show any pure eu-gemini, then one or more interstitial chiasmata in E. M. C. will seldom, if ever, occur. At all events this line of argument indicates that it is highly improbable that the bivalent shown in Fig. 28 *b* has arisen by exchange of segments with the chiasma subsequently terminalised. Of course I do not venture to deny categorically that there is a possibility of a primary association at prophase being able to cause the development of new forms in totally apomictic species, as DARLINGTON assumes, an assumption which I have myself adopted (1934, p. 273). *However, all the gemini that I have hitherto observed in E. M. C. are, from the point of view of the English school of cytologists, with all probability false!*

#### OCURRENCE OF PSEUDO-GEMINI AT METAPHASE IN E. M. C.

In my paper on the origin of new forms I gave an account of the way in which the heterotypic metaphase takes place. Here I shall only examine the importance of association in that division for the conception of chromosome affinity during meiosis.

What guarantees have we that these pseudo-gemini are not fixation artefacts? Objections have already been made, as far as the secondary association is concerned (among others ADATI, 1933), against the highly interesting analysis of the secondary polyploidy in *Pyrus* (1930) made by DARLINGTON and MOFFETT. These workers showed that the probable basic number in the species in question was 7, as in the majority of *Rosaceae*, but ADATI maintained that their results were based on wrong interpretations. It seems to me that DARLINGTON is quite right when he writes that (1932, p. 220): »Secondary pairing, like many peculiarities of chromosome behaviour, is exaggerated in appearance by bad fixation, but its essentially differential character as between different chromosomes cannot be determined by an external agent — it is not an artefact«. Now as regards *Taraxacum* it would be inexplicable if diakinesis in E. M. C. should be free from artefacts, since hardly ever any associations — other than that the chromosomes lying in the vicinity of one another in a few groups of two (or three) — have been observed there. In P. M. C. the diakinetik stages are the most difficult to study, which is at least partly due to the chromosomes clustering together. Further, it appears that in most cases the number of

associations is quite small and varies in different forms and has a definite upper limit (in triploids usually 8), in addition to which they correlate fairly well with the number of primary associations in P. M. C. In E. M. C. the nuclei are also considerably larger than those in P. M. C. and therefore the univalents have a greater possibility of lying scattered and separated from one another. It is evident, as I pointed out in the paper mentioned above, that the formation of pseudo-gemini is due to the fact that single homologous chromosomes happen to lie in the vicinity of each other during diakinesis, and that they arise when the repulsion between the chromosomes on the passage to metaphase decreases and the attraction becomes too powerful.

*As shown by the figures there are all kinds of transitional stages, from complete univalence, free location close to one another, association in which the boundaries between the two chromosomes are not clearly marked, up to formations the appearance of which does not differ at all from terminalised gemini in P. M. C.* On this account I have for the sake of simplicity classified all these pictures under one denomination, pseudo-gemini.

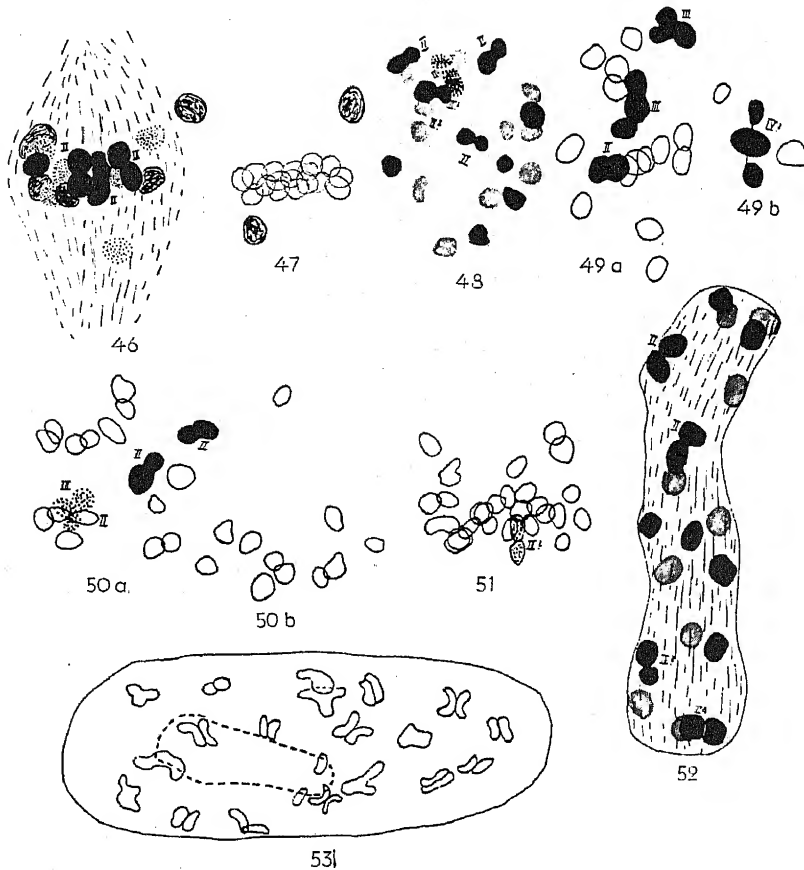
Let us then examine the apomictic plants, the pollen formation of which has already been reviewed. As regards *T. Nordstedtii* and *Kalbfussii* these secondary gemini, which arise at metaphase, are false in the sense that they were not formed by chiasmata, but they are genuine in so far as they are derived from homologous chromosomes. Figs. 40 and 41 show two metaphases, the latter at the point of transition to pseudo-homotypic metaphase. In the former at least two »trivalents» (dotted) and about 11 »bivalents» can be seen. The different degrees of association are seen, from such cases as those at the bottom on the left-hand side *to those cases in which the connection consists of a more or less thin thread and to such cases where the two univalents have »fused»*. In Fig. 41 is seen a probable »tetravalent» (dotted), where the size of the central portion points to its being a »bivalent», associated on both sides with an univalent. In addition there also occur two or three »bivalents». In contradistinction to P. M. C. with its 24 gemini E. M. C. in this autopoloid apomictic species exhibit a considerably reduced formation of bivalents.

This is still more true of *T. Kalbfussii*. Fig. 42 shows 1—3 pseudo-gemini and Fig. 43 shows two. As already mentioned, P. M. C. exhibited here a rather constant number of gemini, 8. Thus in E. M. C. this number drops considerably. In *T. alpinum* ( $\times$  *Pacheri*?), which, as far as P. M. C. is concerned, followed the so-called *Hieracium boreale*



scheme, a large number of E. M. C. were not studied. Fig. 44 shows a metaphase with 2 pseudo-gemini, and such a geminus was also found in another metaphase. Also semi-heterotypic metaphases occur.

The remaining Figures (45—52) show pseudo-gemini from biotypes, the pollen formation of which is not yet known. (Only in



Figs. 46—51. E. M. C. Heterotyp. metaphases. — 46 and 47. 1930: 221. — 48—51. 1930: 712. — Fig. 52. E. M. C. Heterotyp. anaphase. The formation of a restitution nucleus. 1930: 221. — Fig. 53. E. M. C. Interkinesis. 1930: 287. — 2600 X.

*T. ceratophorum* from the Alps I found a high degree of gemini formation. However, owing to bad fixation, no further studies were made.) In Fig. 45 we see three »gemini» from a pseudo-homotypic metaphase in progress. An interesting and valuable observation for the study of the causes of the development of new forms is that these formations are plainly extended along the length of the cell. The same

phenomenon is observed in Fig. 46, which represents a very beautiful pseudo-homotypic metaphase in process of formation. Two or three pseudo-gemini could be discerned here. One chromosome lies apparently outside the spindle, but whether it only appears to do so I cannot decide. By way of comparison Fig. 47 is drawn to show a more advanced stage of pseudo-homotypic metaphase but without any »bivalents».

The highest number of »polyvalent formations» was observed in *T. lactucaceum* ( $2n = 32$ ), and not in *T. Nordstedtii*. Fig. 35 shows a semi-heterotypic metaphase without any pseudo-gemini. Fig. 48 illustrates very beautifully the various degrees of association; we see one pair of chromosomes (II?), the components of which lie a little distance from each other but plainly in the same plane, then two chromosomes close together and finally »bivalents», the parts of which have fused together. In Fig. 49 we see one »tetravalent», two »trivalents» and one »bivalent». The two chromatin threads of the »tetravalent» are plainly discernible. Fig. 50 shows three pseudo-gemini and one pseudo-trivalent, and finally in Fig. 51 are to be seen a pair of chromosomes, plainly aligned in the longitudinal direction of the cell. It must however be remarked that, at the same time as this high degree of association in this form, semi-heterotypic metaphases were observed frequently.

Fig. 52 is in many respects very instructive. It shows a heterotypic anaphase just at the moment when a restitution nucleus is being formed. 2—4 associations were present. One sees how they have been distributed to the two poles. In my paper on the development of new forms I showed (p. 264) that pseudo-gemini, in exactly the same manner as univalents, either wandered across a pseudo-homotypic plate or were distributed to the two poles. No typical *Hieracium boreale* type was ever discovered in E. M. C. Even this argues against the occurrence of primary association at prophase and diakinesis.

The picture also shows that the restitution nucleus is limited and is formed (by »precipitation») of the spindle. The membrane therefore develops at no great distance from the solitary chromosomes, on the contrary several of them can be seen in close proximity to the developed wall. The regularity in the formation of restitution nuclei in E. M. C. in this way acquires its natural explanation. — Only once was a supernumerary nucleus observed in the dyad stage and then in a fixation made at the end of October in order to observe the effect of external factors on the origin of new forms. — For if the method of origin and

the shape of restitution nuclei is induced by the spindle itself it is hardly possible for any irregularities to occur which prevent isolated chromosomes from being embodied in the nucleus. This is in marked contrast to the state of things in P. M. C., where even the formation of restitution nuclei is often of a degenerative nature.

In my paper, already mentioned, I showed how seldom heterotypic anaphases are produced. Nevertheless the restitution nuclei are of an extended shape (only one such figure, 53, is included in this paper, for other reproductions the reader is referred to Figs. 9—12 and 16—18 in the above-mentioned work). Such pictures could be drawn by the hundreds. How can this peculiarity be explained when they still originate so very early? Fig. 52 illustrates this. *Simultaneously with the »precipitation» or alteration in the spindle, which gives rise to the restitution nucleus, there is a violent stretching of the spindle.* In Fig. 52 it can be seen that the spindle has stretched so violently that the central portion has become thinner than the ends. In this way the chromosomes are also pushed from each other quite passively (univalents as well as associations), they are probably not capable of any movement on their own. Figs. 6—8 and 11 in my previous work show only »false» anaphases, in fact they owe their appearance to the stretching of the spindle. The restitution nuclei shaped like an hour-glass, which I have not observed but the occurrence of which is probable from accounts given in the literature, are therefore due to a too severe stretching of the central part of the spindle.

This explanation is entirely in agreement with the views of BELAR (1928) and, later, DARLINGTON (1932). According to this view the univalents in a heterotypic anaphase are not capable of performing any movements of their own, only the bivalent chromosomes are capable of such movements and this due to the repulsion between the spindle attachments. During anaphase the spindle stretches and for that very reason the univalents (divided and undivided) are also frequently incorporated with the two daughter nuclei. We thus see how this view is in complete accordance with the above observations of the shape and formation of the restitution nuclei.

*Taraxacum* exhibits both restitution nuclei and pseudo-homotypic metaphase, in *Antennaria*, *Eupatorium*, etc. only the latter occurs. What is the reason then of the occurrence in E. M. C. in *Taraxacum* of two different methods of acquiring the diploid chromosome number? *It is only during the development of the pseudo-homotypic division that the chromosomes are capable of active movement. During the forma-*

tion of restitution nuclei they only passively obtain their new location. In the former case there occurs an evident further »mitotising» of the already »mitotised» meiosis, as far as pairing is concerned. In the *Antennaria* scheme this unity is undoubtedly genotypically determined, in the *Taraxacum* scheme the properties of the spindle itself (possibly degree of viscosity, electric charge etc.) determines the route of development upon which the E. M. C. enter. Thus it will be seen that this conception also confirms the view held by BELAR and DARLINGTON as to the active importance of the nuclear spindle in the accomplishment of the divisions. That the viscosity in itself is an important feature, I have already pointed out in the work referred to above, since the pseudo-homotypic metaphases contain fewer gemini than the original heterotypic metaphases. — Perhaps then the associations are too heavy or the viscosity of the spindle too great to permit of active movement towards the equator. And this may at the same time be the cause of the formation of restitution nuclei.

Reasoning in this way it is also conceivable that an unequal percentage of restitution nuclei, in proportion to the percentage of pseudo-homotypic metaphases, should also be met with in *Taraxacum*. Observations indicating that this is the case have also been made but I do not venture to express any definite opinion until statistical computations have been made on a large scale.

### THE CAUSES OF THE ORIGIN OF SECONDARY ASSOCIATIONS.

The discovery of secondary associations has already lead to important results: I need only mention the conclusions arrived at by DARLINGTON and MOFFETT (1930) with regard to secondary polyploidy in *Pyrus*, when the writers in question werẽ able to show that the basic number of 17 observed in the *Pomoideae* is only secondary and is derived from the set of 7 which is characteristic of the majority of the *Rosaceae*. A similar deduction was made by MÜNTZING in the potato when he showed that the seemingly basic number of 12 is in reality the tetraploid number (MÜNTZING, 1933). LAWRENCE has in turn endeavoured to prove that secondary association is especially characteristic of allopolyploids with a slight but still discernible homology between the different sets and he therefore considers that the degree of such an association is a measure of the phylogenetic age of the form under examination (LAWRENCE, 1931 c).

LAWRENCE writes (1931 a, p. 288): »But chromosomes which are identical only in minor and scattered portions of their length, may yet have a general affinity which would result in their attraction to one another at certain stages of meiosis». In this paper I have been able to show that where *the genotypic constitution prevents a primary association, secondary associations can occur and that the attraction varies in strength, so causing the occurring pseudo-gemini to differ in appearance*. The possibility of such a more or less threadlike connection between the chromosomes as I have observed here, and which is so beautifully displayed in MÜNTZING's pictures of *Solanum*, is denied by LAWRENCE and DARLINGTON. »In the second case (i. e. in the secondary association)», says LAWRENCE (1931 a, p. 288), »there will be no material connections, and segregation will be unaffected by this secondary association». (Also 1931 b, p. 361.) And in this connection DARLINGTON (1932, p. 221) also writes: »They never touch, except through collapse in fixation; they separate regularly into their daughter halves without interfering with one another». According to the description which I have previously given of this association in *Taraxacum*, conditions are here quite different, without it being possible for that reason to assume that the pictures arising were caused by bad fixation; rather it seems to me that such a difference in attraction as that seen in *Taraxacum* is a consequence of the hypotheses of the English school of cytologists.

During diakinesis in both sexual and apomictic biotypes there is a high degree of repulsion. In the early stages of metaphase this repulsion is suppressed and the diffuse attraction between weakly homologous chromosomes gives rise to the appearance of secondary association. Now inasmuch as the homology between different pairs of chromosomes or univalents varies from case to case (as in *Taraxacum*) there will therefore arise a variation in the attraction. On the one extreme we have those cases in which the chromosomes lie freely in the vicinity of one another without touching, and on the other extreme those cases in which they touch one another or are even fused.

This consequence follows as a result of DARLINGTON's assumption that the chromosomes consist of a pellicle enclosing the chromonema (DARLINGTON, 1932, p. 291). If two chromosomes lie close to one another and attraction occurs between them, then the fusion of pellicles round the four chromatids should result in a reduction of the superficial strain and thus signify a more stable state of equilibrium. Further, on account of the retaining of the terminalised chiasma between the bi-



valent chromosomes at metaphase DARLINGTON is compelled to assume the existence of two kinds of affinity: a terminal and a lateral. Only the end particles of the chromatids possess the former, unlike the intercalary particles which have only the lateral affinity. Hence, there exist, according to DARLINGTON's view, two forces *which can bring about a terminal association in the post-synaptic stage without the necessity (or possibility) of postulating the formation of chiasmata to hold the two chromosomes together*, and therefore in *Taraxacum*, where the normal primary association is suppressed, it should be possible to meet with such a terminal association. There is therefore no need at all to suppose that the touching (and the longer or shorter chromatin-connections) is due to bad fixation. In my paper on the origin of new forms I have already called attention to the different degree of association in *T. dissimile*, where semi-heterotypic metaphase was common and association less frequent, and in 1930:672, where such an occurrence of entirely unpaired chromosomes was never observed at metaphase.

The consequences of this conception are very great for the development of new forms in the totally apomictic species of plants: If the possibility of crossing-over at prophase is out of the question, which is not improbable, then the production of new forms should be contiguous with the occurrence of these secondary associations in the pseudo-homotypic metaphase. This stage follows the heterotypic metaphase. In the majority of cases the spindle attachments should therefore have divided and repulsion between them ensue. Considering the unusually protracted interkinesis in this genus it is not impossible that a relatively long period of time passes after metaphase before the attachments divide; and particularly in such cases where a high degree of secondary association and pseudobivalent-formation occur it is conceivable that this can have a retarding effect on the division of attachments. Further, it is not improbable that the repulsion which usually sets in after the division of the spindle attachment in a chromosome can in certain cases occur between attachments in the two secondarily paired chromosomes! *Hence, even in this respect the pseudo-homotypic metaphase appears to be closely related to heterotypic division, and that pseudo-gemini can behave like eu-gemini, not only with respect to the occurrence of homologous partners.* Finally, it is clear that this non-disjunction of chromatids leads to viable products only where the corresponding (pairing) chromosome is related in substance and thus prevents lethality.

Even in sexual biotypes terminal affinity may result in deceptive formations. Univalents or bivalents can be supposed to associate terminally, the connection even drawn out in the form of a chromatin thread in such a manner that false primary associations may seem to occur. At any rate that possibility is not out of the question, if we only assume with DARLINGTON 1) the occurrence of a pellicle enclosing the chromatin substance, 2) a terminal affinity in the end particles of the chromatids. The study of the »deceptive» meiosis in *Taraxacum* seems to indicate that his assumptions are correct.

### THE SO-CALLED MITOTISING OF PARTHENO- GENETIC E. M. C.

Even if the attraction of the undivided homologous leptotene chromosomes to one another is not considered to be the cause of the formation of chiasmata and the resulting bivalents, still the most important difference between meiosis and mitosis — as DARLINGTON asserts — lies in the difference in time for the longitudinal division of the chromosomes. The mitotic chromosomes divide lengthwise during the resting stage before the following prophase (?), the meiotic chromosomes, on the other hand, divide during this stage. Now since the parthenogenetic processes aim at a development of embryo vegetatively without the agency of fertilisation one might expect to find in apomictic species a substitution of the meiotic nuclear division by a mitotic division, in other words, that they take the step in the opposite direction to that once taken by lower organisms when by means of an incidental precocity they developed meiosis. One expects what is shown by the following scheme:

Mitotically propagating organisms  sexual organisms, with meiosis.  
Mitotically parthenogen. apomictics 

In the higher plants (as in all parthenogenetic apomictic species) it was therefore only necessary for an abandonment of the »acquired» precocity to take place in order to the »mitotising» to be complete. If this had occurred matters would be very simple, indeed, there would no longer be any problem. It would appear as if ROSENBERG's classic study of pollen degeneration in *Hieracium* also supplies a series of phenomena showing the substitution of meiotic division by a mitotic. Only in the most important point do these degenerative phenomena differ from mitosis, they do not attain a somatic longitudinal division

direct, i. e. precocity is not suppressed. The result is the same but the route is different. I have myself shown in *Taraxacum*, which also has an entirely superfluous pollen formation, a series of degenerative phenomena, not in the direction of mitotically divided chromosomes but in the disappearance of the male organ (a now incomplete list of these is found in GUSTAFSSON, 1932 b, p. 111). Neither in this case is there any suppression of precocity. This talk of a mitotising of the meiosis should therefore be regarded sceptically; it is correct in only unimportant points, in the most important point — precocity — it is wrong.

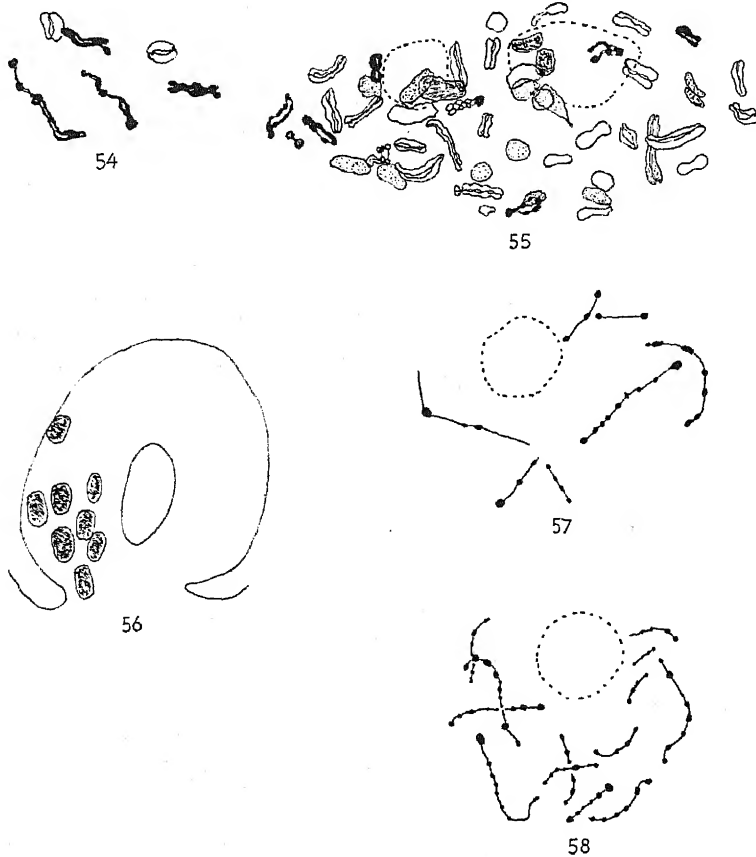
What are the facts then with regard to E. M. C.? Do their stages of development imply a suppression of meiosis in such a manner that they exhibit a retrogression towards mitosis or in such a manner that they constitute a superstructure on meiosis? When *Antennaria alpina* ♀ becomes *A. alpina* ♂ by pseudo-mutation (according to my opinion), it will not be a pure male but an intersex that has lost its vegetative power of propagation. The parthenogenetic E. M. C. thus becomes sexual in the female organ of the intersex but is incapable (owing to disturbed meiosis?) of producing seed. In *A. alpina* ♀ the »apparent mitosis» thus seems to be a superstructure on meiosis.

In the paper mentioned above I showed that the so-called somatic longitudinal division in E. M. C. in the *Antennaria* scheme is not such a division at all. As in the case of *Taraxacum* a pseudo-homotypic metaphase is formed with highly contracted chromosomes, which certainly divide lengthways but are otherwise heterotypic in form. And this longitudinal division is not a sign of a »mitotising»! During heterotypic metaphase in sexual plants the spindle attachments are undivided, but division takes place shortly afterwards (as seen in lagging univalents). Between semi-heterotypic and pseudo-homotypic metaphase there is a longer or shorter period of time, sufficient for the spindle attachments to divide. Strictly speaking the only difference between a sexual semi-heterotypic metaphase and parthenogenetic metaphase (in the *Antennaria* scheme) is that in the latter the anaphase stretching of the spindle is omitted, but this omission does not imply any difference between mitosis and meiosis. *Taraxacum* also exhibits this anaphase stretching, although the formation of restitution nuclei at an early stage prevents the occurrence of the double nuclear stage of the first division.

By losing their precocity the E. M. C. have not reverted to the mitotic stage either. The leptotene stage is rather plainly discernible.



Fig. 57 shows an early stage from *T. Ekmanii* Dr., the threads are undivided, while Fig. 58 shows another from 1930: 123, and these are no exceptional pictures, all early prophases have the same appearance. In the diakinetik stages again, as I have pointed out several times, there



Figs. 54—58. E. M. C. — 54. Unpaired split chrom. from prophase. 1930: 653. — 55. Unpaired chrom. at prediakinetic stage of a hexaploid E. M. C. in the triploid *T. dissimile*. — 56. Hexaploid cells of a triploid ovule. *T. dissimile*. — 57. Early prophase. *T. Ekmanii*. — 58. Early prophase. 1930: 123. — Figs. 54—55, 57—58 2600 X. Fig. 56 about 100 X.

appear very clearly chromosomes divided longitudinally. Fig. 54 shows a few solitary chromosomes at a stage earlier than diakinesis, here they are divided lengthways. It can therefore be assumed that the longitudinal division takes place at a time corresponding to that in sexual plants, but that in spite of this no pairing has taken place be-

tween the undivided chromosomes. (In the literature, for instance, OSAWA, 1913, it is related that synapsis contraction occurs in *Taraxacum*, but I did not observe any in these fixations.) Besides, the strongly pronounced chromosome contraction, present as a rule already at diakinesis, in the dandelions argues against an abandonment of precocity. We know from the investigations of PHILP and HUSKINS (1931) on long-chromosomed *Matthiola* (caused by a recessive gene) that different degrees of chromosome precocity result in varying degrees of univalent formation, and with that irregular pairing of chromosomes and failure of contraction. In *Eupatorium* and *Antennaria* there is indeed no contraction of the chromosomes at diakinesis, but, as in *Taraxacum*, *Chondrilla* and *Erigeron*, it is very marked at metaphase. Hence, there is even here no suppression of precocity!

This brief survey shows, as was pointed out above, that not until a thorough-going investigation has been made will it be possible to approve of the assertion that a suppression of the sexual meiosis is a step backwards in the direction of mitosis. The case of *Antennaria alpina* ♀ — *Antennaria alpina* ♂ shows that the process of mitotic parthenogenesis is possibly a superstructure of meiosis. This also explains why the »mitotised meiosis» has never become a typical mitosis, neither in P. M. C. or E. M. C. At all events the suggested retrogressive step is not so easy to take as — according to DARLINGTON — the step from mitosis to meiosis (DARLINGTON, 1932, p. 307: single mutation, also p. 455).

### THE CAUSES OF THE OMISSION OF PRIMARY ASSOCIATIONS IN E. M. C.

Failure of pairing in sexual biotypes may be due to one of the following causes:

- 1) No homology or defective homology causes univalence of the chromosomes in question. Thus, too few common genes.
- 2) A solitary gene brings about the univalence of the chromosome pair in question.
- 3) A solitary gene brings about complete univalence in the entire set of chromosomes.

(In the last two cases it is immaterial for the argument whether pairing fails owing to delayed precocity or only to lack of chiasmata at prophase.)

Case 2 would be easy to understand. For it is quite natural that the

genes can possess different powers of attraction and that on this account their influence on pairing varies. Case 3, which is practically similar to the conditions in E. M. C. of parthenogenetic apomictic species, is more difficult to understand.

It has already been pointed out that it is not the absence of homology that is the cause of the failure of chromosome pairing in *Taraxacum*. In the male organ in *T. Nordstedtii*, which is probably an autopolyploid, and in *Kalbfussii* there is an extensive formation of gemini, whereas there is no such formation in the female organ. I have observed a similar occurrence in P. M. C. of a form of *T. Vulgaria* with a spontaneous increase in the chromosome number (GUSTAFSSON, 1932 b, Figs. 10—19). Whatever the cause of this may be it is a fact that in one instance (Fig. 19) at least three perfectly homogeneous sets must be supposed to occur without the pairing being increased above the highest number for triploids, 8. — A decisive proof of this is shown in Figs. 55 and 56. In a series of sections of the same ovule from *T. dissimile* cells were observed with doubled chromosome numbers (their location in the different sections is shown in Fig. 56). In E. M. C. from this ovule there were only 24 chromosomes. In another ovule an E. M. C. was found with about 48 chromosomes. Although the nucleus was in early diakinesis no sure bivalents could be observed. Here we therefore have complete evidence proving that there is something in the genotypic constitution which prevents pairing but does not suppress precocity. (Chromosome contraction exists.) Of course chiasma formation is missing, but what is the cause?

CLAUSEN (1930) has related of a case exactly opposed to this. In a form of *Viola Orphanidis* a recessive gene is the cause of an almost complete failure of pairing in the male organ, while in the female organ pairing is normal. What is the cause? »The non-conjugation in the male archesporium must be due to some abnormal physiological conditions there caused by some unbalance in the genic constitution of the plant itself, in other words, it is due to the incompatibility of the whole chromosome complement and not of the individual chromosomes as such. Under better conditions, namely in the female archesporium, the same chromosomes all conjugate.» (CLAUSEN, 1930, p. 70). An account of similar cases has been given by FEDERLEY (1931). In the cross *Pygaera pigra* ( $n=23$ )  $\times$  *P. crutata* ( $n=29$ ) the female has up to 23 pairs while the male is devoid of pairing. The difference is evidently due to a sexually limited quality. (These instances of defective pairing

in the male organ but complete pairing in the female organ could be multiplied many times.)

Conditions are the reverse in *Taraxacum*. In some way or other the genotypic constitution causes a physiological difference between the male and female organs so that pairing is always missing in the latter but without any suppression of precocity. From DARLINGTON's point of view the simplest route to the propagative method of parthenogenetic apomictic species would be simply to «lose» the gene or genes causing the main differences between meiosis and mitosis, the precocity of the former stage. The conclusion that we venture to draw from this is that the route meiosis—mitosis is not so easy to travel and that in all probability the reversible reaction  $\text{mitosis} \rightleftharpoons \text{meiosis}$  is a phylogenetic structure of great complication and which, in addition to the varying degrees of precocity, consists of physiological factors, the nature of which we do not yet understand.

For the question of the origin of parthenogenesis the solving of these problems is of vital importance. It is not impossible that the «parthenogenetic mitotising» of meiosis implies a superstructure of meiosis, not a reversion to somatic mitosis, in other words, that it may be a dominant and not a recessive property. In *Antennaria alpina* ♀ parthenogenesis is dominant and sex-linked, for the false male that is produced, probably by pseudo-mutation, is sexual (although sterile). Perhaps the whole problem of apomixis can be revealed in *Antennaria alpina* ♂.

In conclusion I beg to express my sincere thanks to Dr. H. H. HANDEL MAZZETTI, Vienna, and Dr. G. HAGLUND, Lund, for their assistance in procuring material. I am also very indebted to Dr. A. HÅKANSSON, Lund, for his help and advice concerning the preparations, and to Dr. K. MATJER, Svalöf, for his assistance in the preparation of this paper.

### SUMMARY.

1. *Taraxacum* biotypes with the somatic chromosome numbers 24, 32, 48 are examined.
2. The meiosis in P. M. C. of three biotypes is described. *T. Nordstedtii* has almost complete pairing, *T. Kalbfussii* has about 8 bivalents, and *T. alpinum* (× *Pacheri*?) belongs to the *Hieracium boreale* type.
3. In none of the E. M. C. in which diakinesis had reached its

climax, and so having repulsion between the chromosomes most intense, could the slightest trace of gemini formation be discovered.

4. At metaphase, however, geminilike associations (»bivalents», »trivalents», »tetravalents») have been discovered.

5. Here all transitional stages occur from complete univalence up to formations the appearance of which does not differ from terminalised gemini in P. M. C.

6. It is only during the development of the pseudo-homotypic division that the chromosomes are capable of active movement, during the formation of restitution nuclei they only passively — by the stretching of the spindle — obtain their new location.

7. The leptotene stages and the strongly pronounced chromosome contraction argue against an abandonment of precocity.

8. In some way the genotypic constitution causes a physiological difference between the male and the female organs so that pairing is always missing in the latter but without any suppression of precocity.

9. It is possible that the parthenogenetic »mitotising» of meiosis implies a superstructure of meiosis, not a reversion to somatic mitosis.

Svalöf, 20th of April, 1934.

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# ZUR GENETIK VON PHASEOLUS VULGARIS

## IX. ÜBER DEN EINFLUSS DES GENPAARES R—r AUF DIE TESTAFARBE

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(With a summary in English)

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FÜR die Ausbildung von verschiedenen roten Testafarben bei *Phaseolus vulgaris* ist zuerst von SHAW and NORTON (1918) eine besondere genische Grundlage angenommen worden. Im Kapitel »The Inheritance of Pigments» sagen diese Verfasser (l. c. p. 82): »It is evident that there are two classes of pigments found in the varieties of colored beans used in these experiments. One class appears as some shade of red or purplish red, and is found in Red Valentine, Golden Carmine, Mohawk and similar colored varieties». Und weiter p. 83: »The other class of pigments encountered in this work shows itself in the various shades of yellow, coffee brown and black seen in Giant Stringless, Burpee Stringless and all the Black Wax varieties».

Laut SHAW and NORTON soll das Zustandekommen dieser beiden Serien von Testafarben auf zwei Modifikationsgenen,  $M$  und  $M'$ , zurückzuführen sein.  $M$  soll zusammen mit verschiedenen Farbgenen für die Entstehung der Gelb—Schwarz-Serie verantwortlich sein,  $M'$  für die Ausbildung der Rot- oder Anthocyan-Serie. Für die Entstehung von Marmorierung akzeptieren diese Verfasser die SPILLMAN—EMERSONSche Theorie (EMERSON 1909), laut der jede Marmorierung nur bei Anwesenheit von zwei Genen  $Y$  und  $Z$  auftreten soll, die vollkommene Koppelung aufweisen. In bezug auf eine Kritik dieser, für *Phaseolus vulgaris* nunmehr als überflüssig und unnötig kompliziert zu betrachtenden Theorie verweise ich auf LAMPRECHT 1933.

Ihre Theorie für die Ausbildung verschiedener Testafarben fassen SHAW and NORTON in folgender Weise zusammen (l. c. p. 84): »The production of a totally pigmented bean, then, rests on the presence of several factors. First, we must have  $P$ , in the absence of which we have a white bean; second,  $T$ , in the absence of which the bean has an eye; third, the presence of  $M$  or  $M'$ , the former causing beans of the yellow—black series, and the latter, pigment of the red series. If

neither or only one of the mottling factors  $Y$  and  $Z$  are present the bean is self-colored, while if both are present a mottled bean results. If  $P$  and  $T$  are present,  $M$  and  $M'$  absent, the bean is buff-colored, shown in Blue Pod Butter and the lighter shades in mottled beans».

Für die Ausbildung einer ganzfarbigen Testa wären demnach laut SHAW and NORTON wenigstens zwei Gene,  $P$  und  $T$  erforderlich, und dann sollten die Samen, also mit der Formel  $PP\ TT$ , buff-farbige (roh-seidengelbe oder vielleicht schamois) Testa haben. Aus den Angaben dieser Verfasser geht ferner hervor, dass auch  $PP\ TT\ MM$  buff-farbige Testa bedingen soll, denn S. 86 l. c. sagen sie, dass diese Samenfarbe nur auftritt, »when the modifier  $M$  is absent, or, if present, only when all determiners are absent». Die Annahme des Gens  $M$  und seiner Wirkung gründen diese Verfasser auf die Beobachtung, dass in mehreren Kreuzungen mit der Sorte Blue Pod Butter mit buff-farbigem Samen, in  $F_2$  unter den verschiedenen Testafarben stets etwa ein Viertel wiederum solche Samen hatte.

Welche Farbe  $PP\ TT\ M'M'$  zukommen soll, haben SHAW and NORTON nicht mitgeteilt und anscheinend auch nicht festgestellt.  $PP\ TT$  soll ja buff-farbige Testa verursachen; man hätte da von diesem Rot-Modifizier wohl zu erwarten, dass  $PP\ TT\ M'M'$  eine hellrote Farbe zukommen sollte, die dann durch die Anwesenheit weiterer Farbgene (determiners) vertieft werden könnte.

Die Berechtigung zur Aufstellung der beiden Genpaare  $M-m$  und  $M'-m'$  soll weiter unten im Lichte der von mir erhaltenen Kreuzungsergebnisse diskutiert werden.

Im Jahre 1919 haben TJEBBES und KOOIMAN über eine Kreuzung zwischen »Haricot de Prague marbré nain» mit auf Schamois Grund dunkelrot gestreiften Samen mit einer holländischen Bohnensorte mit hellbraunen Samen berichtet.  $F_1$  hatte Samen, die auf Schamois Grund sowohl braun marmoriert wie violett gestreift waren. In  $F_2$  fanden sie eine Spaltung in 22 hellbraune Samen : 42  $F_1$ -Typus : 27 Dunkelrot auf Schamois gestreift (= de Prague). Die Verfasser nehmen zur Erklärung dieser Spaltung einen Unterschied im Genpaar  $S-s$  an.  $S$  sollte sowohl die Streifung wie die rote Farbe bedingen. Heterozygotie in  $S$  sollte den  $F_1$ -Typus verursachen. Die gefundene Spaltung könnte demnach durch das Verhältnis  $1\ SS : 2\ Ss : 1\ ss$  befriedigend erklärt werden. Diese Spaltung hat auch in der dritten Generation bestätigt werden können (TJEBBES und KOOIMAN 1921 a).

Da KOOIMAN jedoch unterdessen (1920) hat zeigen können, dass Heterozygotie im Genpaar  $B$  (= meinem  $C$ , das Gen, das allein zusam-



men mit dem Grundgen für Testafarbe, *P*, Geschwefeltes Weiss gibt) die in obiger Kreuzung beobachtete Marmorierung bedingt und ferner da Haricot bruns bei Kreuzung mit mehreren anderen Varietäten, die weder *B* noch *S* enthielten, niemals gestreifte Bohnen gegeben haben, sehen sich genannte Verfasser zu einer Revision ihrer Auffassung genötigt und nehmen nun an, dass die obige Kreuzung der Kombination  $BB\ ss \times bb\ SS$  entspricht. Zwischen den beiden Genen *B* und *S* soll vollkommene Koppelung bestehen, und *S* soll, wie bereits vorher erwähnt worden ist, sowohl die Streifung wie die Rotfärbung der Testa verursachen. Gerade dann resultiert die beobachtete Spaltung, nämlich  $1\ BB\ ss : 2\ Bb\ Ss : 1\ bb\ SS$ .

Diese Auffassung behalten die genannten Verfasser in ihren späteren Arbeiten (1921 b, 1922 und 1923) bei, bis der eine von ihnen, TJEBBES (1931) nachweist, dass die rote Streifung der Testa auf zwei Gene zurückzuführen ist, von denen das eine, *S*, die Streifung, das andere, *R*, die rote Färbung bedingt. Die drei Gene *B* ( $= C$ ), *R* und *S* gehören einer Koppelungsgruppe an und zeigen sehr starke Koppelung miteinander. TJEBBES teilt l. c. mit, dass der Crossoverprozent nicht 1 % erreicht.

Von übrigen Verfassern, die sich mit der Vererbung der Testafarbe beschäftigt haben, wird nur das Auftreten von purpurfarbigen, roten oder in diesen Farben marmorierten Samen erwähnt (z. B. SHULL 1907 und 1908), ohne dass weder eine nähere Klassifikation der Farbe noch eine genische Analyse in befriedigender Weise durchgeführt worden ist. Erwähnt zu werden verdient vielleicht eine Arbeit von MIYAKE, IMAI and TABUCHI (1930). In dieser wird u. a. kurz über zwei Kreuzungen berichtet, in denen in  $F_2$  rot gefärbte Samen ausspalteten. Eine Kreuzung »cream  $\times$  white» gab Rötlichpurpur  $F_1$  und in  $F_2$  eine Spaltung im Verhältnis 30 Rötlichpurpur : 6 Purpur : 2 Rot : 19 Cream : 18 Weiss. Eine andere Kreuzung zwischen Rot und Schwarz gab Schwarze  $F_1$  und in  $F_2$  Spaltung nach 184 Rot : 107 Braungelb : 21 Rot : 26 Grau. Es werden nur diese  $F_2$ -Ergebnisse in kürzester Form und ohne irgendwelche Versuche zu einer Erklärung der gefundenen Spaltungsverhältnisse auf genischer Grundlage mitgeteilt. Ohne Kenntnis der Aufspaltung der verschiedenen Testafarben in  $F_3$  und eventuell  $F_4$  erscheint allerdings eine Deutung und Diskussion der erwähnten Resultate auch aussichtslos.

Zusammenfassend kann mit Hinsicht auf bisherige Untersuchungen über das Gen *R* gesagt werden, dass in bezug auf den Einfluss desselben allein sowie im Verein mit einzelnen oder mehreren anderen Farbgenen

auf die Testafarbe nichts sicheres bekannt ist. Es erscheint demnach auch gar nicht erwiesen ob alle Kombinationen von *R* mit anderen Farbgenen rote oder rötliche Nuancen der Testafarbe bedingen. Man kann daher auch noch keineswegs behaupten, dass es zwei verschiedene Serien von Testafarben im Sinne von SHAW and NORTON gibt: eine Gelb—Schwarz-Serie und eine Rot-Serie. Sicher scheint dagegen zu sein, dass *R* mit *C* und *S* sehr stark gekoppelt ist.

### EIGENE UNTERSUCHUNGEN.

Bevor über die mitzuteilenden Kreuzungsergebnisse berichtet wird, sollen hier die beobachteten Testafarben näher charakterisiert werden. Schon früher beschriebene und analysierte werden nur mit Namen und Formel angeführt und sei in bezug auf diese auf LAMPRECHT 1932 und 1933 verwiesen. Bei der Beschreibung der Testafarben wurden die von mir früher benutzten Farben-Arbeiten verwendet, nämlich RC (= Répertoire de Couleurs publié par la Société des Chrysanthémistes et RENÉ OBERTHUR, 1905), CS (= Color Standards and Color Nomenclature by ROBERT RIDGWAY, 1912), FT (= Farbentafeln nach OSTWALD) und CC (= Code des Couleurs, KLINCKSIECK et VALETTE, 1908).

*Geschwefeltes Weiss*, PP CC jj gg bb vv rr, RC 14/3—4.

*Schamois*, PP CC JJ gg bb vv rr, RC 325/1—2.

*Hell Lila*. Die Bezeichnung dieser Testafarbe bezieht sich auf RC Tafel 176. Die am häufigsten vorkommende Nuance dieser Farbe ist Hell Lila, RC 176/1. Die Farbe zeigt im übrigen recht grosse Variation. Die hellsten Nuancen sind noch bedeutend heller als RC 176/1, die dunkelsten, die nur selten vorkommen, gehen bis zu RC 176/4. Weniger gut ausgereifte Samen zeigen ins Bläuliche und Grauliche gehende Nuancen und ab und zu kann man Samen beobachten, die auf einem blassgelblichen (Geschwefeltes Weiss ähnlichem) Grunde einen Hell Lila Anflug aufweisen. Unter gut ausgebildeten Samen können solche vorkommen, bei denen das Lila einen Stich in Lilarosa aufweist und einzelne können eine so dunkel Lila Farbe erreichen, dass sie Dunkel Laelfarbig, RC 187/4 nahekommt. Im CS ist die charakteristische Farbe Light Purplish Vinaceous, XXXIX, 1''' d—f. Variation bis Pale Vinaceous—Lilac, XLIV, 69''' f und Pale Grayish Vinaceous, XXXIX, 9''' f—g (hellste Töne). Unreine Nuancen, infolge weniger guten Ausreifens, sind Pallid Vinaceous—Drab, XLV, 5''' f—g bis Pale Smoke Gray (selten). FT 8,5 cc, sowie etwas heller und dunkler. Samen dieser Farbe haben gleichwie Geschwefeltes Weiss weissen Hilumrand.

*Dunkel Pflaumenviolett.* Die Bezeichnung dieser Farbe ist dem RC entlehnt. Typische Nuance RC 172/4 und noch etwas dunkler. Bei guter Ausreifung zeigt diese Testafarbe keine grössere Variation. Nicht gut ausgefärbte Samen sind heller bis Pflaumenviolett 172/1, ja in vereinzelt Fällen sogar bis Dunkel Lila 176/4. Im CS entspricht die charakteristische Farbe etwa Bordeaux, XII, 71 k—l. Hellere Töne zeigen Übergänge zu Vandyke Red XIII, 1" k—j, schlecht ausgefärbte gehen bis etwas Ocker Red, XXVII, 5" i und noch etwas heller. FT: 8,5 pl bis dunkel 9,0 pn; bei schlechter Ausfärbung heller bis etwa 7,5 ie. Samen dieser Farbe haben braunroten Hilumrand.

Die hier zu besprechende Kreuzung, Nr. 49, wurde ausgeführt zwischen zwei reinen Linien, L 12 und L 29. L 12 stammt aus der bekannten Brechbohnsensorte Canadian Express, deren Samen einfarbige, ganzfarbige, dunkel pflaumenviolette Testa haben. Hilumrand dunkelrotbraun. L 29, die in meinen früheren Arbeiten über die Vererbung der Testafarbe mehrmals erwähnt worden ist, stammt aus der französischen Brechbohnsensorte de la Chine und hat einfarbige, ganzfarbige Samen mit der Testafarbe Geschwefeltes Weiss. Hilumrand nicht gefärbt, Weiss. Dieser Testafarbe entspricht, wie bereits erwähnt, die Formel: *PP CC jj gg bb vv rr*.

Die in Rede stehende Kreuzung wurde 1930 ausgeführt, 1931 wurde  $F_1$ , 1932  $F_2$  und 1933  $F_3$  gebaut. Die auf den Pflanzen der ersten Generation erhaltenen Samen zeigten insofern eine nicht erwartete Testafarbe, als diese bedeutend heller war als die des dunkler gefärbten Elters. Bei der Kreuzung zwischen Linien mit verschiedenen Testafarben war man doch bisher gewohnt, dass auf  $F_1$  die dunklere Farbe dominierte, oder dass eine noch dunklere entstand, oder schliesslich, wenn es zur Ausbildung von heterozygotmarmorierten Samen (*Cc*) kam, dass die Flecken der Marmorierung in ihrer Dunkelheit wenigstens die des dunkleren Elters erreichten. Hier zeigten die Samen die Farbe Schamois mit einer um den Bister Hilumrand beginnenden, gewöhnlich mittelstarken bis schwachen Marmorierung in der Farbe Pflaumenviolett bis sehr hell Pflaumenviolett, die auf den Samen nach unten zu blasser wurde und schliesslich ganz erlosch. Nicht selten war diese Marmorierung nur in unmittelbarer Nähe des Hilumrandes zu erkennen und bei einem geringen Teil der Samen war sie überhaupt nicht sicher zu beobachten.

Die hier beobachtete Marmorierung scheint also von der durch *Cc* verursachten in markanter Weise abzuweichen. Bei letzterer ist eine gut ausgebildete, auf der ganzen Testa gleich starke Marmorierung Regel.

Wenn die in vorliegender Kreuzung beobachtete Marmorierung um den Hilumrand gut ausgebildet ist, scheint sie indessen in ihrer Zeichnung von der Cc-Marmorierung an entsprechender Stelle nicht sicher unterschieden werden zu können. In Fig. 1 sind drei der auf  $F_1$  erhaltenen

TABELLE 1.  $F_2$  der Kreuzung Nr. 49: L 12 aus Canadian Express  $\times$  L 29 aus de la Chine. Die Aufspaltung des Bastarden PP CC Jj gg bb vv Rr, Dunkel Pflaumenviolett/Schamois Rr-marmoriert.

Nr.	Dunkel Pflaumenviolett	Dunkel Pflaumenviolett/Schamois Rr-marmoriert und Schamois	Hell Lila	Hell Lila/Geschwefeltes Weiss Rr-marmoriert und Geschwefeltes Weiss	Summe
3761	3	5	—	—	8
3762	2	5	2	1	10
3763	—	4	—	3	7
3764	3	5	2	2	12
3765	2	3	1	4	10
3766	—	1	2	—	3
3767	1	1	1	—	3
3769	1	3	—	—	4
3770	1	7	1	2	11
3771	4	13	2	6	25
3772	1	8	2	—	11
3773	1	11	—	5	17
3775	—	6	—	5	11
3776	2	5	—	1	8
3777	—	2	1	1	4
3778	2	3	—	2	7
3779	—	4	—	1	5
3780	1	7	1	1	10
3781	—	4	—	1	5
3782	—	2	—	—	2
Summen:	24	99	15	35	173
D/m für	32,44	97,31	10,81	32,44	—
3 : 9 : 1 : 3	1,64	0,26	1,32	0,50	—

Samen abgebildet. Auf den beiden Samen von links in der Figur ist die Marmorierung verhältnismässig stark ausgebildet, am rechten schwach.

Die auf den Pflanzen der zweiten Generation erhaltenen Samen zeigten in bezug auf Testafarbe die in Tabelle 1 mitgeteilten Spaltungsergebnisse. Wie ersichtlich fand eine Aufspaltung in sechs verschiedene Farbentypen statt. Die Tabelle enthält aber nicht sechs diesen ent-

sprechende Kolumnen, sondern nur vier; es wurden nämlich je zwei der gefundenen Farbentypen wegen Klassifikationsschwierigkeiten miteinander vereinigt. Eine befriedigende Erklärung der hier aufgefundenen Spaltung nur auf Grund der  $F_2$ -Ergebnisse wäre nicht gut möglich gewesen. Es soll daher unmittelbar eine schematische Darstellung der Aufspaltung in  $F_2$  dieser Kreuzung, klargelegt durch die Ergebnisse in  $F_3$ , mitgeteilt werden.

Aus der schematischen Darstellung (S. 39) geht hervor, dass es sich hier um eine Spaltung in zwei Genpaaren, nämlich  $J-j$  und  $R-r$  handelt. Dem erhaltenen Bastard wurde die Formel  $PP CC Jj gg bb vv Rr$  zugeschrieben. Beide Elternlinien müssen, da sie farbige Testa

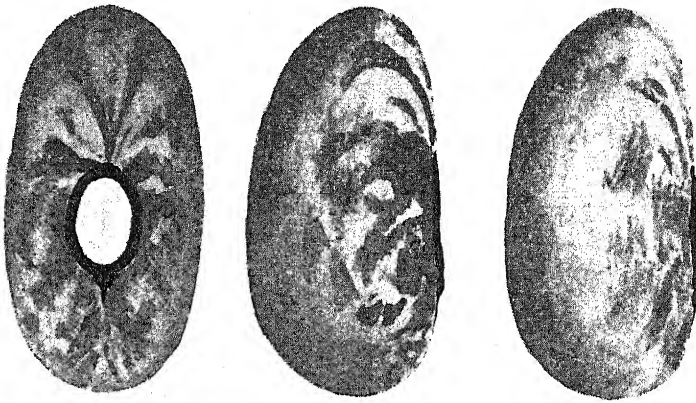


Fig. 1. Drei auf  $F_1$  von Kreuzung Nr. 49 erhaltene Samen mit der Testafarbe Dunkel Pflaumenviolett/Schamois  $Rr$ -marmoriert. Auf den beiden Samen von links ist die  $Rr$ -Marmorierung deutlich, am rechten Samen schwach ausgebildet.

haben, Träger des Grundgens  $P$  für das Auftreten von Pigmentierung sein. Die Konstitution des einen Elters, L 29, ist schon früher einwandfrei nachgewiesen worden (siehe LAMPRECHT 1932, S. 196—201), sie ist  $PP CC jj gg bb vv rr$ . Eine Heterozygotie in  $C$  kann sicher ausgeschlossen werden, denn in  $F_2$  sind nur einfarbige Samen mit der Testafarbe Geschwefeltes Weiss erschienen ( $CC$  entsprechend) und keine Geschwefeltes Weiss/Weiss marmorierten ( $Cc$  entsprechend). Letztere müssten in etwa doppelt so grosser Anzahl als erstere aufgetreten sein, wenn L 12 in ihrer genotypischen Konstitution  $cc$  enthalten würde.

Da also Heterozygotie in  $C$  sicher ausgeschlossen werden kann, darf man unmittelbar schliessen, dass die auf einem Teil der Samen mit den Testafarben Schamois und Geschwefeltes Weiss gefundene, früher beschriebene Marmorierung nichts mit  $Cc$  zu tun hat, sondern,

$F_1$	
$PP\ CC\ Jj\ gg\ bb\ vv\ Rr$	
Dunkel Pflaumenviolett/Schamoiis	
$Rr$ -marmoriert oder Schamoiis	
12 $JJ$ (11,38) mit farbigem Hilumrand	3 $RR$ Dunkel Pflaumen- (2,22) violett
	6 $Rr$ Dunkel Pflaumen- violett/Schamoiis $Rr$ -marmoriert oder Schamoiis
	3 $rr$ Schamoiis
	1 $RR$ Hell Lila (1,39)
4 $jj$ (4,62) mit weissem Hilumrand	2 $Rr$ Hell Lila/Geschwe- feltes Weiss $Rr$ - marmoriert oder Geschwefeltes Weiss
	1 $rr$ Geschwefeltes Weiss
Da phänotypisch nicht immer unterscheidbar, vereinigt: 9 ( $Rr + rr$ ); gefunden: 9,16	
Da phänotypisch nicht immer unterscheidbar, vereinigt: 3 ( $Rr + rr$ ); gefunden: 3,23	

Schematische Darstellung der Aufspaltung des Bastarden  $PP\ CC\ Jj\ gg\ bb\ vv\ Rr$  in  $F_2$  der Kreuzung Nr. 49.  
Die in Klammern und unter gefunden mitgeteilten Zahlen entsprechen den tatsächlich erhaltenen, umgerechnet auf die Kombinationszahl 16.

da *Jj* keine Marmorierung bedingt, auf Heterozygotie in *R* zurückzuführen ist. Eine einwandfreie Bestätigung hierfür bilden die in *F*<sub>3</sub>

TABELLE 2. Spaltungen von Dunkel Pflaumenviolett/Schamois *Rr*-marmoriert in *F*<sub>3</sub> der Kreuzung Nr. 49.

Genotypus in <i>F</i> <sub>2</sub>	Familien- Nr.	S p a l t u n g i n <i>F</i> <sub>3</sub>						
		Dunkel Pflau- menvio- lett	Dunkel Pflau- menviolett/ Schamois <i>Rr</i> -marmo- riert	Scha- mois	Hell Lila	Hell Lila /Geschwe- feltes Weiss <i>Rr</i> - marmo- riert	Ge- schwe- feltes Weiss	Summe
<i>PP CC Jj</i> <i>gg bb vv Rr</i>	8674	8	10	5	1	2	3	29
	8677	3	9	6	3	1	6	28
	8682	1	8	5	1	1	1	17
	8685	8	7	7	—	—	6	28
	8686	6	11	10	2	—	5	34
	8689	6	13	6	1	—	4	30
	8696	5	9	3	4	—	5	26
	8702	5	12	6	—	—	5	28
	8703	6	13	3	3	—	7	32
	8708	3	8	3	3	3	1	21
	8709	5	13	9	—	1	7	35
Summen:	—	56	113	63	18	8	50	308
Erwartet:	—	57,75	176	173,25	19,25	58	57,75	—
D/m für 3: : 9 : 1 : 3	—	0,26	0,26	0,26	0,26	0,04	—	—
<i>PP CC JJ</i> <i>gg bb vv Rr</i>	8664	6	11	10	—	—	—	27
	8667	4	11	3	—	—	—	18
	8668	4	9	9	—	—	—	22
	8688	6	23	7	—	—	—	36
	8700	8	13	9	—	—	—	30
Summen:	—	28	67	38	—	—	—	133
Erwartet:	—	33,25	105	99,75	—	—	—	—
D/m für 3:1	—	1,05	—	—	—	—	—	—

erhaltenen Spaltungsergebnisse. Diese zeigen, dass die marmorierten Samen niemals konstante Nachkommen geben, sondern stets nach dem Verhältnis 1 *RR* : 2 *Rr* : 1 *rr* gespalten haben.

Wie aus Tabelle 1 und der schematischen Darstellung hervorgeht, sind in  $F_2$  zwei verschiedene  $Rr$ -marmorierte Typen aufgetreten, teils Dunkel Pflaumenviolett/Schamois marmoriert und teils Hell Lila/Geschwefeltes Weiss marmoriert. Bei der Aufstellung der  $F_2$ -Resultate in Tabelle 1 sind, wie früher erwähnt worden ist, diese beiden marmorierten Typen mit Schamois bzw. Geschwefeltes Weiss in einer Kolonne vereinigt worden, da die Marmorierung häufig so schwach gewesen ist, dass sie nicht mit Sicherheit festgestellt werden können. Dies gilt ganz besonders für Hell Lila/Geschwefeltes Weiss marmoriert. Eine Vorstellung hiervon bekommt man bei einem Blick auf Tabelle 2, die die Aufspaltung von Dunkel Pflaumenviolett/Schamois in  $F_3$  wiedergibt. Wie aus dieser ersichtlich, sind Spaltungen laut den zwei zu erwartenden Verhältnissen, den Formeln  $PP\ CC\ Jj\ gg\ bb\ vv\ Rr$  und  $PP\ CC\ JJ\ gg\ bb\ vv\ Rr$  entsprechend, vorgekommen. In dieser Tabelle sind die Resultate der Klassifikation entsprechend in 6 Kolonnen mitgeteilt, und erst die Summen für die genannten zwei Paare von Kolonnen sind vereinigt worden.

In der oberen Abteilung der Tabelle, Heterozygotie in den beiden Genpaaren  $J-j$  und  $R-r$  entsprechend, hätten wir eine Spaltung im Verhältnis  $3\ JJ\ RR : 6\ JJ\ Rr : 3\ JJ\ rr : 1\ jj\ RR : 2\ jj\ Rr : 1\ jj\ rr$  zu erwarten (auf die Heterozygotie in  $J-j$  wird wegen vollkommener Dominanz nicht Rücksicht genommen). Wir finden die diesen 6 Genotypen entsprechenden Farben, aber für Schamois einen geringen Überschuss, für Geschwefeltes Weiss einen sehr grossen. Dies besagt, dass die  $Rr$ -Marmorierung auf Schamois in den meisten Fällen festgestellt werden können, auf Geschwefeltes Weiss dagegen nur in wenigen Fällen. Erwähnt sei, dass wenn unter den Samen einer Pflanze auch nur ein einzelner oder wenige Samen eine erkennbare Marmorierung zeigten, diese Pflanze dann als  $Rr$ -marmoriert registriert worden ist. Eine einwandfreie Bestätigung der Erscheinung, dass die  $Rr$ -Marmorierung auf Geschwefeltes Weiss häufig nicht zu erkennen ist, wurde in  $F_3$  erhalten, indem nämlich mehrere Familien, die in  $F_2$  als Geschwefeltes Weiss klassifiziert worden sind, dort nach 1 Hell Lila : 2 Hell Lila/Geschwefeltes Weiss marmoriert : 1 Geschwefeltes Weiss spalteten.

Auch die nach Aussaat der übrigen Typen in  $F_3$  erhaltenen Resultate bestätigen durchweg die oben gemachten Annahmen laut der schematischen Darstellung. So haben Samen mit den Testafarben Dunkel Pflaumenviolett und Hell Lila niemals mehr in bezug auf  $R-r$  Spaltung gezeigt. Sie müssen demnach in  $R$  homozygot sein. Mit der Testafarbe Dunkel Pflaumenviolett wurden in  $F_3$  18 Familien unter-



sucht. Von diesen haben 6, mit zusammen 165 Individuen, konstante Nachkommen gegeben, 12, mit zusammen 295 Individuen, haben im Genpaar  $J-j$  monohybride Spaltung gezeigt. Hierfür wurde erhalten:

Gefunden: 219 Dunkel Pflaumenviolett : 76 Hell Lila  
 Erwartet: 221,25 » » : 73,75 » »  
 D/m für 3 : 1 = 0,31.

Das Verhältnis der konstanten zu den spaltenden Familien stimmt mit dem theoretisch erwarteten (6 : 12) vollkommen überein.

Hell Lila Samen haben, wie erwartet, nur konstante Nachkommen gegeben. Es wurden 11 Familien mit zusammen 293 Individuen untersucht. Schamois Samen haben entweder konstante Nachkommen (2 Familien mit 51 Individuen) gegeben oder im Verhältnis 3 Schamois : 1 Geschwefeltes Weiss gespalten (2 Familien mit 63 Individuen). Samen mit der Testfarbe Geschwefeltes Weiss schliesslich haben — wenn es sich nicht um fehlerhaft als solche klassifizierte  $Rr$ -Samen handelte — nur konstante Nachkommen gegeben (2 Familien mit 69 Individuen).

Zusammenfassend haben die vorstehend mitgeteilten Kreuzungsergebnisse folgendes ergeben. Es wurden vier verschiedene Testfarben mit dem Gen  $R$  nachgewiesen und klargelegt, nämlich:

$PP\ CC\ JJ\ gg\ bb\ vv\ RR$ : Dunkel Pflaumenviolett mit braunroten Hilumrand, die Testfarbe der L 12.

$PP\ CC\ JJ\ gg\ bb\ vv\ Rr$ : Dunkel Pflaumenviolett/Schamois  $Rr$ -marmoriert mit dunkel Bister Hilumrand, oder mit Übergängen bis zu Schamois infolge sehr schwacher Ausbildung der  $Rr$ -Marmorierung.

$PP\ CC\ jj\ gg\ bb\ vv\ RR$ : Hell Lila mit weissem Hilumrand.

$PP\ CC\ jj\ gg\ bb\ vv\ Rr$ : Hell Lila/Geschwefeltes Weiss  $Rr$ -marmoriert mit weissem Hilumrand, oder (häufig) mit nicht mehr erkennbarer  $Rr$ -Marmorierung: Geschwefeltes Weiss.

Es wurde eine für *Phaseolus vulgaris* bisher nicht mitgeteilte Art von Marmorierung festgestellt, die durch Heterozygotie im Genpaar  $R-r$  bedingt wird. Ob dies stets der Fall ist, kann natürlich nicht gesagt werden, da bisher nur 2 Genotypen diesbezüglich untersucht worden sind. Diese Heterozygotmarmorierung ist — wenigstens in den

hier studierten Fällen — häufig schwach ausgebildet; namentlich gilt dies für den Genotypus *PP CC Rr*. Bei mehr oder weniger deutlicher Ausbildung derselben ist sie nicht gleichmässig über die Testa ausgebreitet, sondern auch solchenfalls nur in der Nähe des Hilumrandes deutlich zutage tretend.

Mit Berücksichtigung des Umstandes dass nun zweierlei Arten von Heterozygotmarmorierung bekannt sind, verursacht durch Heterozygotie teils in *C—c*, teils in *R—r*, sollen diese beiden Arten von Marmorierung, um Unklarheiten zu vermeiden, im weiteren als *Cc*-Marmorierung und als *Rr*-Marmorierung bezeichnet werden.

Das Genpaar *R—r* bedingt also in den mitgeteilten Fällen eine Spaltung nach dem *Zea*-Typus, in Übereinstimmung mit dem Verhältnis  $1 RR : 2 Rr : 1 rr$ . Da der heterozygote Typus *Rr* dem durch *rr* bedingten Typus deutlich näher steht, ja in gewissen Fällen von letzterem nicht unterschieden werden kann, könnte die Ausbildung von Testafarben mit rotem Einschlag (Dunkel Pflaumenviolett, Hell Lila) auch als rezessiv bedingt aufgefasst werden.

Die Resultate vorliegender Kreuzung (die Testafarben Hell Lila und Hell Lila/Geschwefeltes Weiss *Rr*-marmoriert) zeigen, dass das Farbgen *R* — in Übereinstimmung mit den beiden Farbgenen *C* und *V* — keine Färbung des Hilumrandes verursacht. Die übrigen drei Farbgene von *Phaseolus vulgaris*, *J*, *G* und *B*, verursachen je bekanntlich eine solche.

Schliesslich sprechen die Kreuzungsergebnisse dafür, dass die beiden Genpaare *J—j* und *R—r* unabhängig voneinander vererbt werden.

Wir wollen nun die einleitend mitgeteilten, von SHAW and NORTON (1918) in bezug auf die Ausbildung der Testafarben gemachten theoretischen Grundlagen einer kurzen kritischen Diskussion unterziehen. Diese Verfasser nehmen an, dass es zwei verschiedene Serien von Testafarben gibt, eine Gelb—Schwarz-Serie und eine Rot-Serie, für deren Zustandekommen das Vorhandensein im ersteren Falle eines Gens *M*, im letzteren eines Gens *M'* Grundbedingung sein sollte. Verschiedene weitere Gene (determiners) sollten zusammen mit diesen die verschiedenen Testafarben verursachen. Samen nur mit dem Grundgen für Pigmentierung, *P*, oder mit *P* und *M* sollten Buff-Farbe (Rohseidengellb, Ecreu) haben.

In bezug auf *M* sei das Resultat einer von mir früher veröffentlichten Kreuzung (LAMPRECHT 1932, S. 196—201) angeführt. Diese

Kreuzung, Nr. XII: Geschwefeltes Weiss,  $PP\ CC \times$  Rohseidengelb (= Buff),  $PP\ JJ$ , hat in  $F_1$  Schamois/Rohseidengelb  $Cc$ -marmorierte Samen gegeben und in  $F_2$  eine klare Spaltung in folgendem Verhältnis:

3 $PP\ CC\ JJ$ : 6 $PP\ Cc\ JJ$ : 3 $PP\ cc\ JJ$ : 1 $PP\ CC\ jj$ : 2 $PP\ Cc\ jj$ : 1 $PP\ cc\ jj$					
Schamois	Schamois/ Rohseiden- gelb $Cc$ - marmoriert	Rohseiden- gelb	Geschwefel- tes Weiss	Geschwefel- tes Weiss/ Weiss $Cc$ - marmoriert	Rein- weiss

Die Richtigkeit der Auffassung dieser  $F_2$ -Spaltung wurde durch die in  $F_3$  erhaltenen Spaltungen einwandfrei bestätigt.

Dieses Resultat dürfte genügen um die Annahme eines Gens  $M$  im Sinne von SHAW and NORTON unmöglich zu machen. Erstens sehen wir, dass der Grundfaktor  $P$  allein keine Buff-Farbe verursacht, wie diese Verfasser l. c. annehmen, sondern überhaupt keine Färbung der Testa bedingt. Laut den genannten Verfassern sollten hier überhaupt keine reinweissen Samen ausspalten können. Zweitens sollte bei Richtigkeit der Annahme von SHAW and NORTON, wenn  $J$  für Buff-Farbe mit  $M$  identisch wäre, eine Spaltung in sowohl  $J$  wie in dem einen determinier  $C$  zu erwarten sein, was in einem Spaltungsverhältnis 9 verschieden gefärbte : 7 Buff-farbige resultieren müsste. Nichts von alledem ist eingetroffen. Die oben angeführte Spaltung lässt demnach die Annahme eines Gens  $M$  als Bedingung für das Zustandekommen der Testafarben der Gelb—Schwarz-Serie laut SHAW and NORTON unmöglich erscheinen. Die in Frage stehende Spaltung erfährt durch die Annahme des Zusammenwirkens der beiden Farbgene  $C$  und  $J$  mit dem Grundgen, wie dies im  $F_2$ -Spaltungsverhältnis oben angeführt ist, ihre durchweg befriedigende Erklärung. Auch in allen anderen von mir untersuchten Kreuzungen, mit bisher über 200.000 Nachkommen, hat sich diese Annahme als stichhältig erwiesen.

Ähnlich verhält es sich mit der Annahme des Gens  $M'$ , das für die Entstehung der Testafarben der Rot-Serie laut SHAW and NORTON verantwortlich sein sollte. Die vorstehend besprochene Kreuzung Nr. 49 zeigt klar, dass es sich beim Auftreten von roten Tönen — wenigstens im hier mitgeteilten Fall — stets um Zusammenwirken des Farbgens  $R$  mit dem Grundgen  $P$  und anderen Farbgenen handelt. Man könnte vielleicht geneigt sein,  $R$  mit  $M'$  identifizieren zu wollen. Auch dies erscheint unmöglich, denn es gibt Samen mit  $R$  und  $P$  in ihrer Konstitution, bei denen von irgendeinem roten Einschlag in der Farbe nichts entdeckt wird. So erhielt ich nach Kreuzung der Sorte Hinrich Riesen

mit rosarot gestreiften Samen mit meiner Linie 108 mit Glauescens-Samen, entsprechend den genischen Formeln  $PP RR SS \times PP VV ss$  auf  $F_1$  rein Tiefgrau gestreifte Samen, auf Grund deren Testafarbe man nicht auf den Gedanken der Anwesenheit eines Gens für Rot-Färbung kommen konnte, was laut SHAW and NORTON der Fall sein sollte. Das Angeführte dürfte genügen um die Unhaltbarkeit der Annahme der beiden Gene  $M$  und  $M'$ , mit der ihnen von den genannten Verfassern beigelegten Wirkungsweise, darzutun.  $M$  ist hierbei nicht mit dem Gen für Homozygotmarmorierung zu verwechseln, das schon früher von anderen Verfassern mit diesem Buchstaben bezeichnet worden ist.

### SUMMARY.

1. In the introduction the author gives a survey of what has been published hitherto on the subject of the influence exercised by the  $R$  gene on the seed coat colour in *Phaseolus vulgaris*. In this connexion an account is given of the results of a cross, in which a segregation takes place in two colour genes, viz.  $R$  and  $J$ . On the basis of these results the author arrives at the following conclusions:

2. The genotypic constitution of  $PP CC JJ gg bb vv RR$  causes the seed coat colour of Bordeaux (RIDGWAY, 1912, XII, 71 k—l), that of  $PP CC jj gg bb vv RR$  the seed coat colour of Light Purplish Vinaceous (RIDGWAY, 1912, XXXIX, 1''' d—f).

3. In heterozygosity in  $R$  there occurs a more or less evident marbleization, broken off from the hilum downwards; in the former case (under par. 2) of Bordeaux on Chamois, in the latter, of Light Purplish Vinaceous on Primrose Yellow (in accordance with RIDGWAY, 1912). In the latter case the marbleization is often so feeble that it cannot be established with certainty.

4. Hence, there are two different marbleizations known in *Phaseolus vulgaris*, occasioned by heterozygosity in colour gene. With respect to the genes in question they will in future be designated as  $Cc$  and  $Rr$  marbleization respectively.

5. On account of the frequently poor effect of  $Rr$  — at least in the cases examined here — the two red colours mentioned might also be regarded as recessively conditioned characters.

6. Seeds having the colour Light Purplish Vinaceous, corresponding to the formula  $PP CC jj gg bb vv RR$ , have shown themselves to possess a white hilum margin, which can be taken as evidence that the gene  $R$  does not cause any coloration of this area.

7. The results of crossing experiments seem to point to the fact that the *J* and *R* genes are inherited independently of each other.

8. In conclusion the author shows that the two genes *M* and *M'*, assumed by SHAW and NORTON (1918), the former being considered responsible for the formation of a yellow—black series, the latter for the formation of a red series of seed coat colour, must now be regarded as non-existent. All the seed coat colours established genotypically by the author hitherto (in all about 60 different colours) have been thoroughly explained by various combinations of the six colour genes *C*, *J*, *G*, *B*, *V* and *R* together with the two modifying genes *Vir* and *Och*. Further, it has been proved that there does not exist any red series of seed coat colour in connexion with any definite gene, the *R* gene, which in several cases causes shades of red, in certain combinations with the other colour genes giving rise to colours in which no trace of red can be seen.

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# ZYTOLOGISCHE STUDIEN ÜBER SEXUELLES UND ASEXUELLES *HIERACIUM UMBELLATUM*

VON *BENGT BERGMAN*

STOCKHOLM

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## MATERIAL UND METHODE.

UNTER den Archieracien ist *Hieracium umbellatum* eine der wenigen bisher bekannten sexuellen Arten. Von diesem kennt man indessen schon seit langem eine apomiktische Form und zwar var. *linearifolium*, die zytologisch von ROSENBERG (1917, 1927 b) untersucht worden ist. Als ich im Sommer 1932 eine Untersuchung von *H. umbellatum* von verschiedenen Orten von einem gewissen Gesichtspunkt in Angriff nahm, fand ich noch eine apomiktische Form, die nach Kastrierung unbehindert Früchte ansetzte. Sie stammt aus Klutchi im zentralen Kamtschatka, wo sie von Dr. R. MALAISE im August 1926 eingesammelt worden ist. Sie ist im Hortus Bergianus in Stockholm aus Samen aufgezogen worden. In Dr. E. HULTÉNS »Flora of Kamtschatka and the adjacent Islands« (1930) ist sie unter der Einsammlungsnummer 319 aufgenommen; HULTÉN gibt aber nicht genauer an um welche Form es sich handelt, sondern sagt sowohl von ihr als auch von mehreren anderen aus Kamtschatka: »Here as well as in other countries it is very variable and the specimens enumerated above belong to several different forms. The species is thus taken here in the wide sense.« (HULTÉN 1930, S. 234.) Eine genauere Bestimmung oder Beschreibung derselben habe ich noch nicht fertig gebracht, aber dass sie zum Formenkreis von *H. umbellatum* gehört ist zweifellos, was von Professor G. SAMUELSSON in Stockholm freundlichst kontrolliert worden ist. Ich nenne sie bis auf weiteres *H. umbellatum forma*.

In der vorliegenden Untersuchung ist auch eine von mir in der Nähe von Stockholm fixierte sexuelle Form von *H. umbellatum* behandelt worden und zum Teil sind Vergleiche zwischen den zytologisch-embryologischen Verhältnissen der beiden vorgenommen worden.

Das Material wurde teils mit Nawaschins Chromsäure-Essigsäure-Formalin, teils mit Carnoys Alkohol-Chloroform-Eisessig fixiert. Als Färbungsmittel gelangten Newtons Gentiana-Violett (für Wurzelspitzen

und Reduktionsteilung) und Heidenhains Eisenhämatoxylin mit Lichtgrün als Kontrastfarbe (für Embryologie) zur Verwendung.

### CHROMOSOMEN.

Die zytologischen Verhältnisse, die man bei der apomiktischen *umbellatum*-Form antrifft, stimmen in ihren wesentlichen Zügen mit denen überein, die ROSENBERG (1917, 1927 a) in seinen bekannten Untersuchungen über die Archieracien beschrieben hat. Ich habe demnach reichlich Gelegenheit gehabt die semiheterotypische Teilung und die Restitutionskernbildung zu studieren, werde mich aber nicht dabei aufhalten, da Professor ROSENBERG gegenwärtig eine neue Arbeit über diese vorbereitet. Ich habe aber auch einige andere zytologische Beobachtungen gemacht, über die ich Bericht erstatten will, da sie von gewissem Interesse sind.

Die sexuellen Archieracien haben bekanntlich die Chromosomenzahl  $2n = 18$  und die apomiktischen im allgemeinen  $2n = 27$ . Dies gilt auch für die beiden von mir untersuchten *umbellatum*-Formen. Die sexuelle hat  $2n = 18$  und die apomiktische  $2n = 27$  (+ einem kleinen Fragment). Die eine ist also diploid, die andere triploid (was auch bei der apomiktischen var. *linearifolium* der Fall gewesen ist; ROSENBERG 1917, 1927 a). Wenn es sich um eine derartige Polyploidieerscheinung bei Pflanzenformen handelt, die derselben Art angehören, hat man ja Ursache von vornherein Autopolyploidie zu erwarten, und eben um eine eventuelle Bestätigung derselben in dem in Frage stehenden Falle zu finden hatte ich eigentlich diese Untersuchung begonnen, da die Frage nach Auto- oder Allopolyploidie vom allgemein apomiktischen Gesichtspunkt aus von grosser Bedeutung ist.

Um diese Sache zytologisch zu untersuchen kann man in zweierlei Weise vorgehen. Man kann einerseits die somatische Chromosomenmorphologie der beiden Formen vergleichen, andererseits die Bindungsverhältnisse in der Reduktionsteilung untersuchen.

Das Studium der Morphologie der somatischen Chromosomengarnituren erwies sich in diesem Falle als äusserst mühsam. Die Chromosomen sind nämlich ziemlich lang und gleichartig und in der Metaphasenplatte liegen sie grossenteils im Gesichtsfeld nach aufwärts oder abwärts gekrümmt. Es ist mir deshalb auch nicht gelungen ein vollständiges Chromosomenidiogramm der beiden Formen aufzustellen.

In der Chromosomengarnitur der sexuellen Form sind es indessen zwei besondere Chromosomenpaare, die infolge ihres von den übrigen

abweichenden Aussehens relativ leicht zu identifizieren sind und ich habe mich deshalb darauf beschränkt die Chromosomengarnitur der triploiden Form in bezug auf diese zu untersuchen.

Fig. 1 A zeigt eine somatische Metaphasenplatte ( $2n = 18$ ) aus einer Wurzelspitzenzelle der sexuellen Form. Die betreffenden Chromosomenpaare sind in der Figur voll gezeichnet. Wie man sieht, ist das grössere Paar sehr leicht an seinen Satelliten wiederzuerkennen. Das andere Paar gehört der kleinsten Grössenordnung an und die Chromosomen sind winklig umgebogen (wahrscheinlich mit einer medianen Konstriktion). Man sieht, dass die anderen Chromosomen im übrigen recht gleichartig sind und keine besonderen morphologischen Charaktere aufweisen.

Was nun die triploide Form betrifft, so ist ihre somatische Chro-

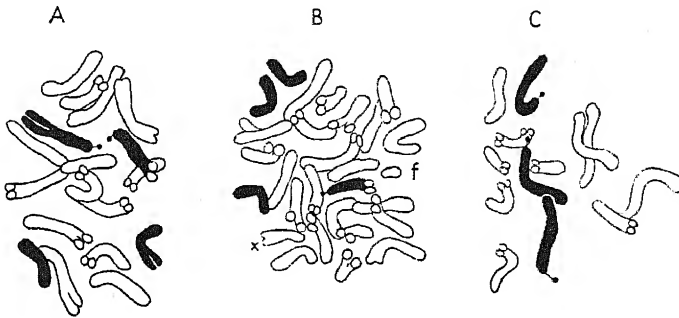


Fig. 1. *H. umbellatum*. Somatische Metaphasen. A, sexuelle Form. — B—C, asexuelle Form. *f*, das Fragment, *x*, das fragmentierte Chromosom. —  $\times 2150$ .

mosomengarnitur (ebenfalls von einer Wurzelspitzenzelle) in Fig. 1 B abgebildet und ein Teil derselben aus einer anderen Zelle in Fig. 1 C. Die kleinen winklig umgebogenen Chromosomen (in Fig. 1 B vollgezeichnet) kommen hier, wie ersichtlich, in Dreizahl vor. Von den Satellitenchromosomen sieht man in dieser Fig. nur eines, aber dass auch diese in Dreizahl vorkommen ist aus Fig. 1 C zu ersehen, die einen Teil einer angeschnittenen Chromosomenplatte wiedergibt. Ich habe mich durch Untersuchung einer grossen Anzahl von Metaphasenplatten davon überzeugt, dass diese beiden Chromosomentypen immer in Dreizahl auftreten.

Wie aus den verschiedenen Figuren hervorgeht, stimmen diese beiden Chromosomentypen ihrem Aussehen nach vollkommen mit den entsprechenden bei der diploiden Form überein und ich halte es für sehr wahrscheinlich, dass die triploide Form aus drei einander mor-



phologisch ähnlichen Genomen aufgebaut ist, von denen jedes einzelne seinerseits mit der haploiden Garnitur der diploiden Form gleichartig ist.

Es ist indessen nicht möglich, ausschliesslich aus diesen Verhältnissen den Schluss zu ziehen, dass wir es in der apomiktischen Form mit einem Autotriploid zu tun haben, da man die Chromosomenmorphologie überhaupt bei keinem anderen Archieracium kennt. Jedenfalls sprechen diese Verhältnisse nicht gegen eine derartige Auffassung. Bei weitem aufschlussreicher sind jedoch diesbezüglich die Verhältnisse in der Mikrosporogenese, auf die ich gleich eingehen werde.

Wie schon früher erwähnt worden ist, enthält die apomiktische Form ein Fragment (Fig. 1 B). Das Fragment ist in der Fig. mit *f* bezeichnet und das vermutlich fragmentierte Chromosom mit *x*. Gerade wegen seiner ungewöhnlich geringen Grösse bin ich der Ansicht, dass das Fragment von diesem mit *x* bezeichneten Chromosom herstammt. Es ist in allen (aus ca. zehn Individuen stammenden) Wurzelspitzen angetroffen worden, die ich untersucht habe; aber hinsichtlich seines sonstigen Auftretens innerhalb der apomiktischen Form kann ich mich nicht äussern.

Diese Fragmentierung bei einer apomiktischen Pflanze ist von einem gewissen Gesichtspunkt aus bemerkenswert. Sie zeigt, dass eine derartige Pflanze beispielsweise durch Fragmentierung das Aussehen ihrer ursprünglichen Chromosomengarnitur verändern kann. Infolge ihrer apomiktischen Natur werden diese Veränderungen unverändert weitervererbt, oder sozusagen »akkumuliert«. Eine z. B. ursprünglich autopolyploide, apomiktische Pflanze kann also nach einem derartigen Vorgang in ihrer somatischen Chromosomengarnitur Allo- oder Aneuploidie zum Ausdruck bringen. Das ausschliessliche Studium der somatischen Chromosomenmorphologie kann diesbezüglich also in gewissen Fällen zu fehlerhaften Schlussfolgerungen führen.

In der Mikrosporogenese herrscht gewöhnlich vollständige Asynthese zwischen sämtlichen Chromosomen. Der normale Verlauf ist demnach eine semiheterotypische Teilung, die entweder zur Bildung von Restitutionskernen oder Polyaden führt. Fig. 2 A zeigt eine derartige Teilung. Man sieht, dass das Fragment (in der Fig. *f*) sich ebenso verhält wie die übrigen Chromosomen. Diese sind meistens stark kontrahiert wie in einer normalen Meiosis, können aber bisweilen doch somatisiert sein, wie aus Fig. 2 B hervorgeht. Eines der Chromosomen macht sogar den Eindruck mit einem Satelliten versehen zu

sein, was also als ein Glied in dieser Somatisierung zu betrachten wäre. Der Satellit ist indessen im Präparat nicht ganz überzeugend und da ich in anderen, ähnlichen Fällen keinen solchen gefunden habe, handelt es sich wahrscheinlich um ein kleines Fragment.

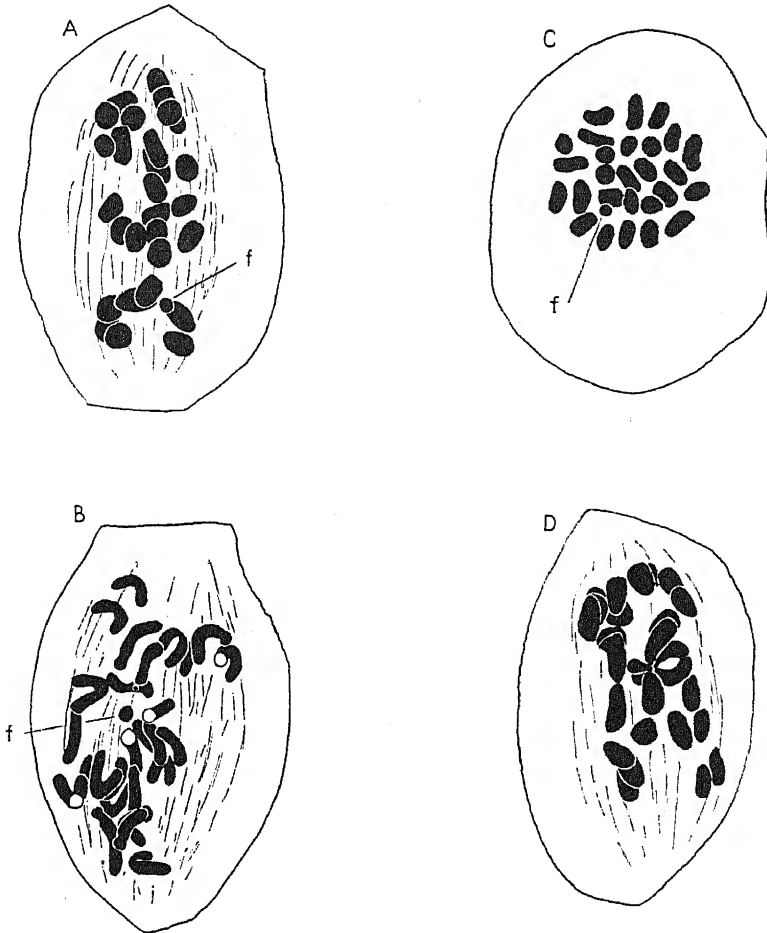


Fig. 2. *H. umbellatum*. Asexuelle Form. Pollenmutterzellen in Teilung. A, eine semiheterotypische Anaphase. B, eine semiheterotypische Teilung mit langgestreckten Chromosomen. Kommt seltener vor. C, eine Metaphase, wahrscheinlich von einem Restitutionskern. D, ein Fall von schwacher Konjugation. Zwei Gemini und ein »Trisom« (s. Text) sind ausgebildet worden. f, das Fragment. —  $\times 2150$ .

Auch ROSENBERG hebt hervor, dass eine derartige Somatisierung der Chromosomen in der semiheterotypischen Teilung bisweilen vorkommen kann. Er sagt: »In einigen Arten, wie z. B. *H. intybaceum*, kann die Gestalt der Chromosomen etwas wechseln, indem dieselben

dort oft ziemlich langgestreckt erscheinen (vgl. Fig. 6)». (ROSENBERG 1927 a, S. 313).

Fig. 2 C zeigt eine Metaphasenplatte mit recht stark kontrahierten Chromosomen, die wahrscheinlich von einem Restitutionskern herkommen.

Bei Untersuchung einer grösseren Anzahl von Pollenfächern findet man indessen, dass die Asynthese nicht in allen P. M. Z. vollständig durchgeführt ist. So findet man, dass in manchen von ihnen eine wirkliche Konjugation stattfindet. Diese Fälle treten freilich mehr vereinzelt auf, aber ich habe mich ihnen doch speziell gewidmet und bin dabei zu einem recht interessanten Resultat gekommen.

Eine derartige Konjugation ist übrigens auch von ROSENBERG bei einigen anderen Archieracien, die dem *levigatum*-Typus angehörten, wahrgenommen worden. Er sagt: »Nun kommt es nicht allzu selten vor, bei Arten wie *H. alpinum*, *levigatum*, *umbellatum* (apomikt. Form), dass in den Pollenfächern der äusseren Blüten eines Köpfchens, wo die meisten P. M. Z. schon zu degenerieren beginnen, einige, plasmareiche P. M. Z. noch bestehen, die frei und abgerundet sind. Deren Kerne sind eben in der ersten Teilung begriffen. Und dabei sind merkwürdigerweise einige Gemini-Chromosomen deutlich zu erkennen; die Teilung folgt also dem *Boreale*-Typus». Er setzt dann fort: »Das Vorkommen solcher verspäteten Teilungen erklärt sich dadurch dass während der wie oben gezeigt, sehr frühzeitig einsetzenden semiheterotypischen Teilung dieselbe nicht gleichzeitig alle P. M. Z. eines Antherenfaches betrifft. Gruppen von 3—5 P. M. Z. mit den Kernen in Ruhestadium kommen hier und da zwischen in Teilung begriffenen vor. Später und fast nur in den Randblüten gehen diese P. M. Z. in die Teilung über, wenn die meisten anderen P. M. Z. schon aufgelöst sind. Und bei dieser Teilung werden, wie gesagt, einige Gemini gebildet. Interessant ist, dass es fast immer nur die Randblüten sind, die eine solche Geminibildung zeigen». (ROSENBERG 1927 a, S. 318). Diese Konjugation tritt auch bei der von mir untersuchten apomiktischen Form vorzugsweise in den P. M. Z. der äusseren Blüten auf, aber inwiefern diese P. M. Z. in ihrer Teilung den übrigen im Fache gegenüber verspätet sind, habe ich nicht mit Bestimmtheit entscheiden können. Ich habe ausserdem auch das eigentümlich gruppenweise Auftreten derselben konstatieren können. So kommen immer 3—5 nahe aneinander liegende P. M. Z. vor, die gleichzeitig Konjugation aufweisen. (Vgl. auch *Eupatorium glandulosum*, HOLMGREN 1919).

Der Umfang der Konjugation in diesen P. M. Z. kann sehr wech-

selnd sein. So zeigt Fig. 2 D einen Fall mit schwächerer Konjugation. Es sind nur zwei Gemini ausgebildet sowie ein eigentümliches Trisom, das dadurch entstanden ist, dass das Fragment sich als drittes einem Geminus angeschlossen hat.

Von Interesse ist indessen, dass in gewissen P. M. Z. mit stärkerer Konjugation wirkliche Trisome gebildet werden (Fig. 3 A—E). Fig. 3 A—C zeigt drei solche Trisome aus drei verschiedenen Metaphasen-

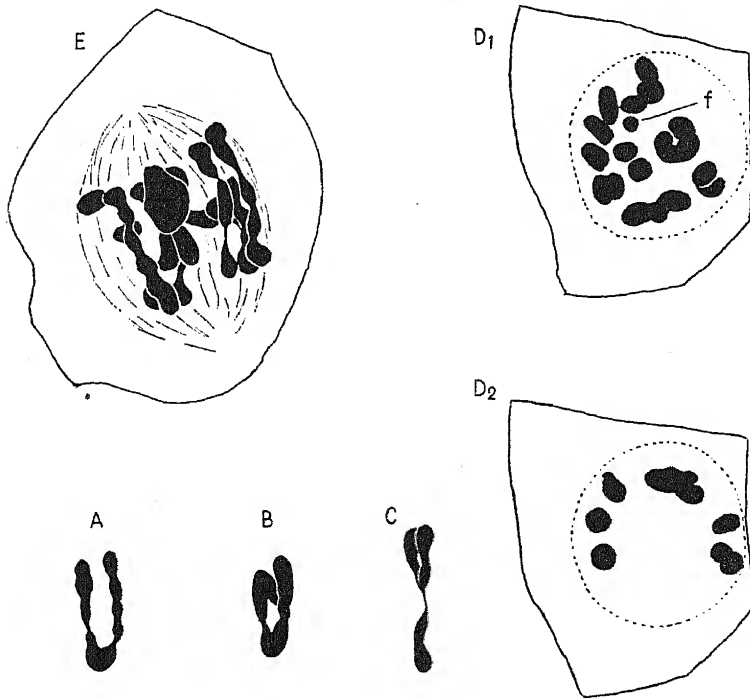


Fig. 3. *H. umbellatum*. Asexuelle Form. A—C, Trivalente aus verschiedenen Metaphasenplatten.  $D_1$ — $D_2$ , eine Diakinese mit vier Tri-, zwei Bi- und zehn Univalenten. E, eine Metaphase mit vier oder fünf Trivalenten. f, das Fragment. —  $\times 2150$ .

platten, Fig. 3 C ein y-förmiges, Fig. 3 A und B zwei v-förmige. Fig. 3  $D_1$  und  $D_2$  stellen eine späte, beim Abzeichnen auf zwei Figuren verteilte Diakinese mit vier Trivalenten, drei Bivalenten und zehn Univalenten dar, von denen einen das Fragment ist. Fig. 3 E zeigt eine (etwas angeschnittene) Metaphase in Seitenansicht mit vier oder fünf Trivalenten (drei kettenförmigen, einer y-förmigen und möglicherweise einer ringförmigen).

Sowohl die starke Trivalentenbildung als auch das Resultat, zu

dem das Studium der somatischen Chromosomen geführt hat, deutet meines Erachtens darauf, dass wir es in der Chromosomengarnitur des apomiktischen *H. umbellatum* mit drei homologen Genomen zu tun haben oder mit anderen Worten, dass es sich wirklich um ein Autotriploid handelt, das wahrscheinlich aus einer sexuellen *umbellatum*-Form durch Kopulation eines haploiden und eines diploiden Gameten entstanden ist. (Vgl. WINKLER 1920.)

### EMBRYOLOGIE.

Ferner habe ich eine Untersuchung der Entwicklung des weiblichen Gametophyten bei den beiden Formen vorgenommen und bin beim Vergleich zwischen ihnen zu einem recht unerwarteten Resultat gekommen.

Der E. S. des sexuellen *H. umbellatum* entwickelt sich nach dem für die Kompositen charakteristischen »Normalschema« und das Resultat ist ein normal organisierter, achtkerniger E. S. mit drei Antipodenzellen, welche letztere von sehr kurzer Lebensdauer sind. Bezüglich der Endosperm Bildung bei den Archieracien liegen nur von einem Verfasser Angaben vor.

MURBECK (1904) teilt nämlich mit, dass ehe der Eikern sich zu teilen begonnen hat 8—16 Endospermkerne auftreten, zwischen welchen erst später Zellulosewände angelegt werden. Also von Anfang an nukleares Endosperm (vgl. jedoch DAHLGREN 1920). Ferner hat er zwar nicht gesehen, dass die Polkerne mit einander verschmelzen, aber er hält es für wahrscheinlich.

Bei einer Untersuchung der Endosperm Bildung des sexuellen *H. umbellatum* erhielt ich zuerst den Eindruck, dass es sich von vornherein um eine zelluläre Endosperm Bildung handelte, da schon die Vierkernstadien deutliche Wände aufwiesen. Als ich indessen zufälligerweise ein Zweikernstadium fand (Fig. 4 A<sub>1</sub>), zeigte es sich, dass diesem jeder Ansatz zu einer Wand fehlte. Eine erneuerte Prüfung der Vierkernstadien ergab, dass bei gewissen von ihnen nur zwei Wände ausgebildet waren, wodurch eine zentrale zweikernige Zelle entstanden war. Es ist also wahrscheinlich, dass die primäre Wand, die durch die erste Teilung des Zentralkerns hätte angelegt werden sollen, erst während der späteren Phase des Vierkernstadiums ausgebildet wird. Wir haben es also hier mit einem von Anfang an nuklearen Endosperm in seiner reduziertesten Form zu tun, das ausschliesslich das erste Zweikernstadium umfasst.

Das entsprechende Stadium bei der apomiktischen Form ist in Fig. 4  $B_1$  abgebildet. Wie aus dieser hervorgeht, wird die erste Teilung des Zentralkerns von einer Wandbildung begleitet, was ich Gelegenheit hatte in noch ein paar Fällen zu kontrollieren. Die betreffende Wand

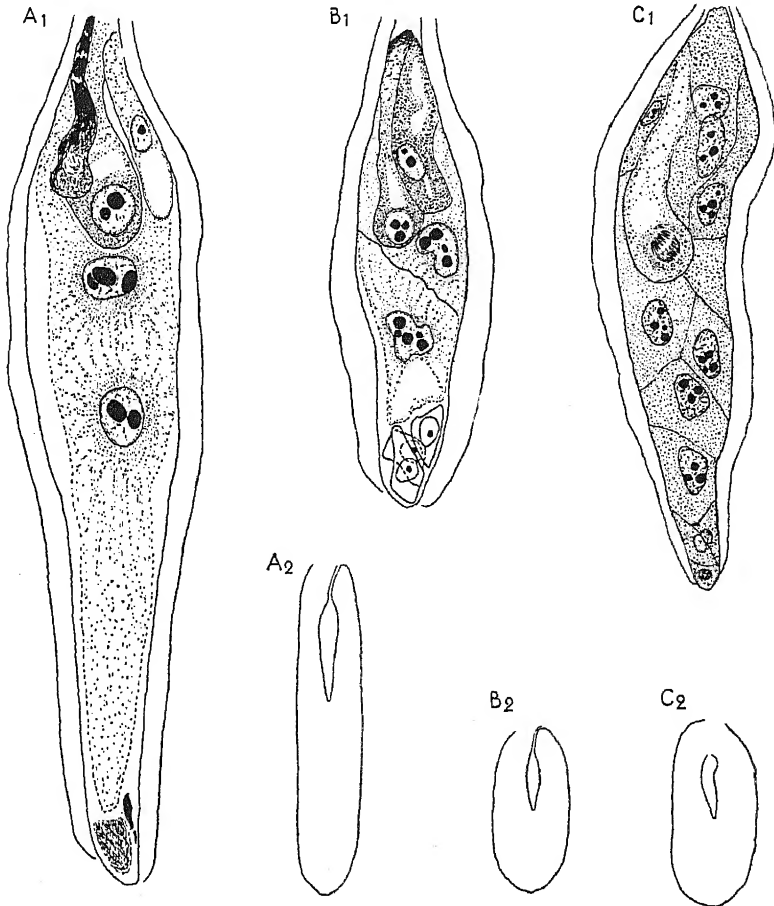


Fig. 4. *H. umbellatum*. Embryosäcke mit angefangener Endospermbildung. —  $A_1$ — $A_2$ , sexuelle Form. Nukleare Endospermbildung.  $B_1$ — $B_2$  und  $C_1$ — $C_2$ , asexuelle Form. Zellulare Endospermbildung. In  $C_1$  hat der Eikern sich zu teilen angefangen. —  $\times 335$ .

steht in der Fig. schief im Verhältnis zur Längsrichtung des E. S. Inwiefern dies verallgemeinert werden kann, wage ich nicht zu entscheiden. Ich habe jedoch einen Fall gefunden, wo sie senkrecht zur Längsrichtung des E. S. gestellt war.

Die Polkerne verschmelzen immer miteinander, wenigstens in allen

Fällen, die ich Gelegenheit zu kontrollieren hatte. So habe ich wiederholt die Verschmelzung selbst gesehen oder auch durch Chromosomenzählungen in den Endospermkernen darauf geschlossen. Der Antipodenapparat besteht auch hier aus drei Zellen.

Die sexuelle und die apomiktische Form unterscheiden sich demnach bezüglich der Endospermbildung voneinander. Erstere hat von Anfang an nukleares, letztere zelluläres Endosperm. Dass diese Ver-

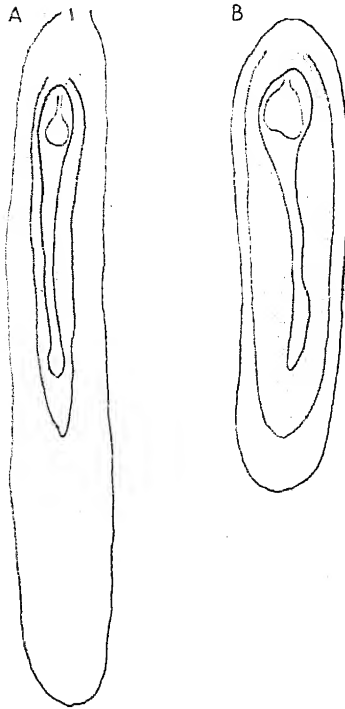


Fig. 5. *H. umbellatum*. Ältere Samenanlagen. A, sexuelle Form. B, asexuelle Form. —  $\times 40$ .

änderung des Endospermbildungstypus bei der apomiktischen Form direkt oder indirekt mit ihrer triploiden oder apomiktischen Natur zusammenhängt, ist wohl wahrscheinlich (oder kommen beim sexuellen *H. umbellatum* Formen vor, die sich hinsichtlich der Endospermbildung verschieden verhalten?).

Bei einem Vergleich zwischen Fig. 4 A<sub>1</sub> und B<sub>1</sub>, die bei gleicher Vergrößerung gezeichnet sind, fällt der beträchtliche Grössenunterschied zwischen diesen beiden E. S. auf. Der E. S. der sexuellen Form ist während des Befruchtungsstadiums durchweg ungefähr doppelt so gross wie der der asexuellen Form im entsprechenden Stadium (s. Fig.). Dies beschränkt sich indessen nicht nur auf die Embryosäcke selbst, sondern gilt für die ganzen Samenanlagen. Das geht aus Fig. 4 A<sub>2</sub> hervor, welche ein Übersichtsbild des E. S. in Fig. 4 A<sub>1</sub> mit der

dazugehörigen Samenanlage gibt und entsprechend verhält es sich mit Fig. 4 B<sub>1</sub> und B<sub>2</sub>. Ungefähr die gleichen Verhältnisse herrschen noch nachdem der Eikern bei der apomiktischen Form sich zu teilen begonnen hat und die Endospermbildung relativ weit vorgeschritten ist (ca. 16 Kerne), wie aus Fig. 4 C<sub>1</sub> sowie aus dem Übersichtsbild 4 C<sub>2</sub> hervorgeht. Der E. S. ebenso wie die ganze Samenanlage hat jetzt unterdessen angefangen an Umfang zuzunehmen und in dem Entwicklungsstadium des Embryos, das Fig. 5 darstellt, hat der E. S. bei der apomiktischen Form (B) ungefähr gleiche Grösse wie der der sexuellen

Form (A). Die Samenanlage ist im ganzen aber noch kleiner und ob sie überhaupt dieselbe Grösse erreicht wie bei der sexuellen Form kann ich nicht feststellen, da ich über keine so alten Stadien verfüge.

Man könnte vielleicht erwarten, dass auch die jüngeren Samenanlagen bis zu dem neuorganisierten E. S. bei den beiden Formen einen beträchtlichen Grössenunterschied in korrespondierenden Stadien aufweisen würden. Dieser ist indessen nicht nennenswert. Die Ursache für die Grössendifferenz in den Fällen von Fig. 4  $A_1$  und  $B_1$  ist statt dessen in folgendem zu suchen.

Nachdem bei der sexuellen Form der junge, achtkernige E. S. sich organisiert hat (wobei er ungefähr gleiche Grösse wie der E. S. in Fig. 4  $B_1$  hat) beginnt er ebenso wie die ganze Samenanlage zuzuwachsen und wird erst befruchtungsreif wenn er die Grösse erreicht hat, die Fig. 4  $A_1$  zeigt. (Diese Erscheinung ist schon von AFZELIUS [1924] bei *Senecio* und anderen sexuellen Kompositen beschrieben worden.) Bei der asexuellen Form hingegen verschmelzen die Polkerne nach Fertigstellung des E. S. sofort miteinander und der Zentralkern macht ebenfalls sofort einige Teilungen durch, worauf der Eikern sich zu teilen beginnt. Mittlerweile hat auch hier in der ganzen Samenanlage ein Zuwachs begonnen, entsprechend dem bei der früher genannten Form, was später, wie schon erwähnt, zu einem Ausgleich der Grössenverhältnisse führt. Bei der sexuellen Form ist es offensichtlich, dass die Samenanlage sowie die ganze Blüte eine gewisse Entwicklung erreichen muss, einen gewissen Reifegrad, damit die erforderliche Pollinierung eintreten kann. Bei der asexuellen Form, die von einer solchen Pollinierung unabhängig ist, kann dagegen die weitere Entwicklung im E. S. unmittelbar einsetzen. Bemerkenswert ist also, dass der Eikern bei der apomiktischen Form sich in einem bedeutend früheren Entwicklungsstadium der Blüte zu teilen beginnt als bei der sexuellen.

Ich habe jetzt von der Ausgestaltung des weiblichen Gametophyten bei dem apomiktischen *H. umbellatum* und den damit in Zusammenhang stehenden Erscheinungen gesprochen, aber noch nichts von ihrem frühesten und sehr wichtigen Stadium, der ersten Teilung der E. M. Z. gesagt.

Diese war sehr schwer aufzufinden und erst nach vielem Suchen fand ich einige Prophasenstadien derselben, die indessen hinreichend instruktiv waren um die Natur der ersten Teilung verständlich zu machen.

Fig. 6 A zeigt das Stadium, in dem man gewöhnlich den Kern der E. M. Z. antrifft. Wie man sieht befindet sich der Kern sogar hier im



Ruhestadium, obwohl die E. M. Z., oder richtiger, der einkernige E. S. zu wachsen begonnen, schon die Nuzellusepidermis durchbrochen hat und ein gutes Stück gegen die Mikropyle vorgedrungen ist. Gleich nach diesem Stadium tritt der Kern indessen endlich in die Prophase der ersten Teilung ein und eine solche ist in Fig. 6 B abgebildet. Man sieht, dass er bedeutend an Umfang zugenommen hat und dass seine Form gegen die Enden hin zugespitzt ist. Bemerkenswert ist indessen die langgestreckte Form der Chromosomen, die zeigt, dass die Teilung somatischer Natur ist, identisch mit der schon von HOLMGREN (1919)

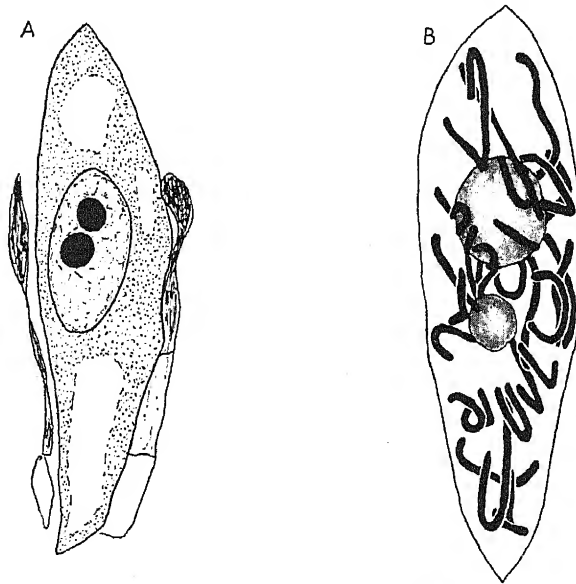


Fig. 6. *H. umbellatum*. Asexuelle Form. A, die E. M. Z. ist direkt zu einem einkernigen E. S. geworden. Der Kern im Ruhestadium.  $\times 840$ . B, der Kern in der Prophase der ersten Teilung.  $\times 2150$ .

bei *Eupatorium glandulosum* und von STEBBINS (1932) bei einigen apomiktischen *Antennaria*-Arten beobachteten. Derselbe Teilungstypus tritt bestimmt auch in der Regel bei *Antennaria alpina* auf, obwohl JUEL (1900) ihn seinerzeit anders deutete. Alle die oben erwähnten Verfasser haben auf die starke Verspätung der ersten Teilung der E. M. Z. in den betreffenden Fällen aufmerksam gemacht, die wie aus dem vorhin Gesagten hervorgeht, auch bei der apomiktischen *H. umbellatum*-Form vorkommt. Die weitere Entwicklung erfolgt dann ebenso wie bei anderen Archieracien nach dem *Antennaria*-Schema (ROSENBERG 1930).

STEBBINS (1932) hat indessen die wichtige Beobachtung gemacht,

dass ausser dieser rein somatischen Teilung bisweilen ein anderer Teilungstypus in der E. M. Z. bei den von ihm untersuchten apomiktischen *Antennaria*-Arten auftritt. Er sagt von diesem »second type«, wie er ihn nennt: »The second type occurs much less frequently, but some stages of it were found in each of the seven species. Here there is a definite spireme in the young megaspore mother cell (fig. 32), and the spireme contraction or synizesis is present (fig. 33). Diakinesis occurs at the same stage as in the non-parthenogenetic species, but both paired and unpaired chromosomes are present, while the nucleus is very large (fig. 8). At the heterotypic metaphase there are a few chromosomes at the equator (fig. 9), but the majority are scattered irregularly over the spindle«. (STEBBINS 1932, S. 328). Bei diesem Typus sind, wie aus seinen Figuren hervorgeht, die Chromosomen auch stark kontrahiert, wie in einer gewöhnlichen Meiosis. Die Teilung ist also von derselben Natur wie in der P. M. Z., wenngleich mit bedeutend stärkerer Asyndese. Sie stimmt demnach am ehesten mit dem *H. boreale*-Typus überein und resultiert ebenso wie dieser im allgemeinen in Polyadenbildung. Dieser Typus bildet also eine vollständige Abweichung von dem gewöhnlichen *Antennaria*-Schema und führt wahrscheinlich zu Sterilität dieser Samenanlagen.

Dass eine ähnliche Veränderung der somatischen Teilung in der E. M. Z. in heterotypischer Richtung bisweilen auch bei dem apomiktischen *H. umbellatum* vorkommt, darauf kann ich aus mehreren »Anomalien« in gewissen Samenanlagen schliessen. Fig. 7 stellt einige solche dar. Fig. 7 A zeigt eine Pentade, Fig. 7 B eine Dyade, bei welcher letzterer der mikropylare Kern offensichtlich eine grössere Portion Chromosomen erhalten hat als der basale. In Fig. 7 C sind ein oder zwei mikropylare Megasporen aufgetreten, die jedoch durch die in kräftigem Zuwachs begriffene basale verdrängt worden sind. Fig. 7 D zeigt eine vollständig regelmässige Dyade, die wahrscheinlich aus einem Restitutionskern entstanden ist. Diese Fälle entsprechen vollkommen dem Resultat der Teilungen in den P. M. Z. und stimmen auch in ihren Hauptzügen mit den betreffenden Fällen bei STEBBINS' *Antennaria*-Arten überein, weshalb anzunehmen ist, dass ihnen eine Teilung von mehr heterotypischer Natur vorangegangen ist. Noch eine Erscheinung, die dafür spricht, zeigt Fig. 7 E, nämlich einen vereinzeltten Fall von Synapsis, den ich gefunden habe und der es wahrscheinlich macht, dass den abweichenden Teilungen ein derartiges Stadium vorausgeht, was hier sonst in den E. M. Z. nie vorkommt. In den P. M. Z. tritt es hingegen

regelmässig auf und auch dem »second type» STEBBINS ging Synapsis voraus.

Aus dem oben Gesagten geht hervor, dass die somatische Teilung in der E. M. Z. bei dem apomiktischen *H. umbellatum* aller Wahrscheinlichkeit nach bisweilen einen mehr heterotypischen Charakter annimmt. Diese Fälle müssen indessen relativ selten sein und dürften 1 % nicht übersteigen. Dessen ungeachtet muss man ihnen eine gewisse Bedeutung für die Pflanze zuschreiben, seit DARLINGTON (1930, 1932) darauf hingewiesen hat, dass wir bei diplo-parthenogenetischen Pflanzen sehr

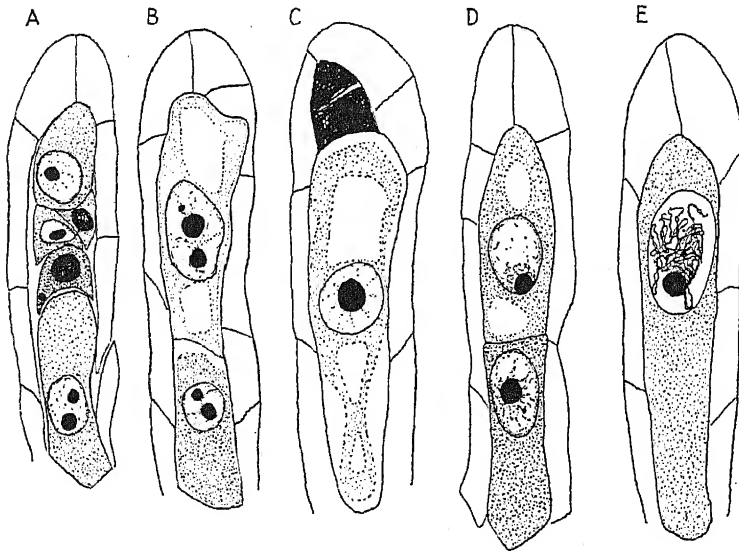


Fig. 7. *H. umbellatum*. Asexuelle Form. A—D, die E. M. Z. hat eine »anomale» Teilung erfahren. A, eine Pentade. B, eine Dyade. Der mikropylare Kern ist bedeutend grösser. C, ein basales Megaspore verdrängt einige mikropylare. D, eine regelmässige, möglicherweise aus einem Restitutionskern entstandene Dyade. E, ein vereinzelter Fall mit der E. M. Z. in Synapsis. —  $\times 840$ .

gut eine Abspaltung haben können, die der Mendelspaltung bei den sexuellen entspricht, freilich in begrenzterer Form. Die Voraussetzung dafür, dass eine solche eintritt, ist, dass wenigstens ein Chromosomenpaar konjugiert (sodass die Möglichkeit für Crossing-over vorliegt) und dass Restitutionskernbildung eintritt. Beide diese Voraussetzungen sind nun bei STEBBINS' apomiktischen *Antennaria*-Arten vorhanden und auch bei dem von mir untersuchten apomiktischen *H. umbellatum*, da die somatische Teilung in der E. M. Z. mitunter in heterotypischer Richtung verändert werden kann. Wenn sich herausstellen sollte, dass die meisten anderen apomiktischen Archieracien eine durchaus somatisierte Teilung

lung in der E. M. Z. haben (was ich für wahrscheinlich halte), so braucht das also nicht zu bedeuten, dass die rein zytologischen Voraussetzungen für eine Abspaltung bei ihnen fehlen. Sie können sich sehr leicht wie das asexuelle *H. umbellatum* verhalten.

Bei einem Vergleich zwischen Fig. 7 A—D einerseits und Fig. 6 A andererseits findet man, dass die erste Teilung der E. M. Z. in den ersteren Fällen bedeutend früher eingetreten sein muss als dies in dem letzteren der Fall sein wird. Auch STEBBINS sagt bezüglich »the second type»: »Diakinesis occurs at the same stage as in the non-parthenogenetic species», also liegt auch hier keine Verspätung vor, wenn die Teilung heterotypischen Charakter annimmt. Das legt die Vermutung nahe, dass ein gewisser kausaler Zusammenhang zwischen der somatisierten Teilung in der E. M. Z. und der starken Verzögerung derselben vorliegt. Wenn man sich auf den Standpunkt von DARLINGTONS precocity-Theorie stellt, kann man auch zu einem derartigen Zusammenhang gelangen wie ihn DARLINGTON (1932) schildert. Eine Verspätung der Meiosis müsste demnach seiner Meinung nach zu einem Mangel an »precocity» führen, was Asyndese und auch Somatisierung der Chromosomen mit sich bringen würde.

ROSENBERG (1917, 1927 a) hat darauf hingewiesen, dass die P. M. Z. bei den apomiktischen Archieracien ihre Teilung in einem relativ frühen Entwicklungsstadium der Antheren beginnen, während die P. M. Z. noch in intimen Kontakt miteinander liegen. Das konnte ich auch bezüglich des asexuellen *H. umbellatum* konstatieren. Bei diesem herrschen also ganz verschiedene Verhältnisse in der männlichen und der weiblichen Sporenmutterzelle. Im ersteren erfolgt die erste Teilung zu früh, im letzteren bedeutend verspätet und die so ganz verschiedenen Chromosomentypen in den beiden Sporenmutterzellen sind wohl auch diesem Umstand zuzuschreiben.

### SCHLUSSBEMERKUNGEN.

Die hier für das asexuelle *H. umbellatum* beschriebenen zytologischen Verhältnisse deuten ja auf Autopolyploidie hin. Auf zytologischer Grundlage ist, soweit mir bekannt, bisher nur MÜNTZING (1931) zu derselben Auffassung hinsichtlich gewisser apomiktischer, polyploider *Potentilla*-Biotypen gekommen. Sonst herrscht ja gewöhnlich die Auffassung, dass die apomiktischen Pflanzen allopolyploid und durch eine Artbastardierung entstanden sind (vgl. jedoch WINKLER 1920 und ROSENBERG 1930).

Bei einer autopolyploiden Pflanze hat man eine starke Affinität

zwischen den Chromosomen in der Reduktionsteilung sowie Multivalentenbildung zu erwarten. Beim asexuellen *H. umbellatum* kommt dies, wie wir gesehen haben, nur ausnahmsweise vor. In der Regel herrscht statt dessen eine vollständige Asyndese zwischen allen Chromosomen. Diese Asyndese kann indessen hier nicht auf mangelhafte Homologieverhältnisse zurückzuführen sein, da wir es aller Wahrscheinlichkeit nach mit drei homologen Genomen zu tun haben. Es muss also eine andere Ursache vorliegen und es kann wohl kaum einem Zweifel unterworfen sein, dass hier eine genbedingte Asyndese vorliegt. Von genbedingter Asyndese sind nunmehr verschiedene Fälle bekannt: *Drosophila* (GOWEN 1928), *Datura* (BLAKESLEE 1928), *Zea* (BEADLE 1930) und *Hordeum* (EKSTRAND 1932). Es kann vielleicht von gewissem Interesse sein, wenn ich in diesem Zusammenhang mitteile, dass auch ich selbst in diesem Jahre eine derartige bei *Leontodon hispidus* gefunden habe. Nun muss man natürlich annehmen, dass die Asyndese beim asexuellen *H. umbellatum* mit seiner apomiktischen Natur zusammenhängt. Das Primäre bei jeder Apomixis der Art, wie sie bei *Archieracium* vorkommt, ist selbstverständlich die Aufhebung der Reduktionsteilung und die Voraussetzung dafür ist eben Asyndese. Ich glaube daher annehmen zu dürfen, dass das Gen (oder die Gene) für Apomixis und Asyndese in diesem Falle sehr nahe miteinander verbunden oder gar identisch sind. Die disharmonischen Verhältnisse, die in der Reduktionsteilung bei den meisten apomiktischen Phanerogamen auftreten, brauchen daher nicht als ein Zeichen für eine vorübergegangene Artbastardierung aufgefasst zu werden (vgl. auch BEADLE 1930, S. 20). Manche von diesen Pflanzen können sicher Autopolyploidie derselben Natur wie das asexuelle *H. umbellatum* aufweisen.

### ZUSAMMENFASSUNG.

1. Eine neue apomiktische Form von *Hieracium umbellatum* ist angetroffen worden.
2. Ein Studium der somatischen Chromosomen und der Verhältnisse in der Reduktionsteilung hat erwiesen, dass es sich aller Wahrscheinlichkeit nach um eine autotriploide Form handelt.
3. In der Mikrosporogenese herrscht gewöhnlich vollständige Asyndese zwischen allen Chromosomen. In einigen Ausnahmefällen findet jedoch eine Bindung statt.
4. Die Endosperm bildung ist bei der asexuellen Form von vorn herein zellular, bei der sexuellen nuklear.

5. Der Eikern beginnt bei der asexuellen Form sich in einem bedeutend früheren Stadium in der Entwicklung der Blüte zu teilen als bei der sexuellen.

6. Die erste Teilung der Embryosackmutterzelle ist bei der asexuellen Form rein somatisch und es geht ihr ein längeres Ruhestadium voraus.

7. Es ist der Gedanke ausgesprochen worden, dass die Asyndese bei der asexuellen Form genbedingt ist und dass das Gen (oder die Gene) für Asyndese und Apomixis in diesem Falle sehr nahe miteinander verbunden oder gar identisch sind.

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Meinem verehrten Lehrer Herrn Professor Dr. O. ROSENBERG sage ich hiermit meinen besten Dank für das Interesse und all die Hilfe, die er meinen Untersuchungen stets zuteil kommen liess. Herrn Professor Bergianus Dr. ROBERT E. FRIES bin ich für sein Entgegenkommen, mir das Untersuchungsmaterial zur Verfügung zu stellen, Dank schuldig.

Stockholm, Botanisches Institut der Universität, Mai 1934.

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# THE NEGATIVE CORRELATION OF CHIASMA FREQUENCIES

BY K. MATHER AND R. LAMM

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IT has been shown that if crossing over be suppressed, by the use of inversions, in two of the major chromosomes of *Drosophila melanogaster* crossing over is significantly increased in the other chromosome (REDFIELD, quoted by MORGAN, BRIDGES and SCHULTZ 1933). This appears to imply a negative correlation between the cross over frequencies of the different chromosomes in the same cell at meiosis, *i. e.* a unitary, or at least partially unitary control of crossing over in the cell. — (There is an alternative explanation of this result, *viz.* that the progeny, which are regular, must contain X and III chromosomes which have been paired at meiosis, since failure of pairing leads to non-disjunction which, at least for the third chromosome, is lethal in its effects. Now pairing at metaphase of meiosis is only by chiasmata and, on the chiasmatype theory, chiasmata represent cross overs. Hence there may be selection for modifiers increasing the frequency of crossing over. Which is the correct explanation is impossible to say, but it seems very probable that both play a part. This second explanation cannot be applied to the cytological results, however.)

Now on the basis of the partial chiasmatype theory of chiasma formation, as advocated by DARLINGTON (1932), and also on the basis of BELLING's theory (1933), both of which maintain that chiasma formation is conditioned by crossing over, there should be a similar negative correlation between the frequencies of chiasma formation in the bivalents at the first meiotic division. Since meiosis in *Drosophila* females cannot be studied, evidence on this point must be derived from elsewhere. The results given below were obtained in another connection but are amenable to analysis from this point of view.

In the vast majority of organisms it is impossible to distinguish individually all the bivalents at the stages of meiosis when chiasmata are present, but two methods are available for the detection of correlations if they exist. First, in those organisms in which it is possible to pick out any single bivalent, the chiasma frequency of this one may be correlated against the total chiasma frequency of the remaining bi-



valents. This method may be extended to those cases in which more than one bivalent is distinguishable but it must not be applied in those cases where there is a special length pairing relationship, such as often accompanies great size differences. The second method is applicable to those cases in which the chromosomes are all of the same size or very nearly so. It consists in determining the presence of intra-class correlations by the use of the analysis of variance (FISHER 1928). The former method has been applied by DARLINGTON (1933) to rye with eight, instead of seven, bivalents at meiosis. The extra bivalent is very

TABLE 1.

	B i v a l e n t s							C e l l s													
	0	1	2	3	4	5	6	Total	11	12	13	14	15	16	17	18	19	20	21	22	Total
<i>Secale</i> , plant 1	1	31	138	68	7	—	—	245	2	—	1	8	8	7	3	5	1	—	—	—	35
» » 2	—	8	155	64	4	—	—	231	—	1	—	1	10	13	3	4	1	—	—	—	33
» » 3	—	30	153	60	2	—	—	245	—	—	4	10	8	10	2	1	—	—	—	—	35
» » 4	1	20	83	120	21	—	—	245	—	—	—	1	1	6	4	6	12	4	1	—	35
» » 5	1	21	82	132	9	—	—	245	—	—	—	—	1	3	16	6	7	1	1	—	35
» » 6	—	4	150	89	2	—	—	245	—	—	—	1	3	12	14	5	—	—	—	—	35
» » 7	—	25	102	111	7	—	—	245	—	—	1	1	1	6	17	7	2	—	—	—	35
» » 8	—	30	118	88	9	—	—	245	—	—	—	1	9	11	12	1	1	—	—	—	35
» » 9	1	16	94	45	12	—	—	168	—	—	—	1	9	6	5	2	—	—	1	—	24
<i>Secale</i> , long bivalents of DARLINGTON (1933) .....	1	16	134	78	23	—	—	252	—	—	2	2	5	3	11	8	2	—	2	1	36
<i>Vicia m</i> chromosomes ...	—	3	16	126	85	18	2	250	—	—	1	1	2	10	18	11	6	1	—	—	50

small, is quite easily recognised and shows no sign of special pairing relationships. He found a negative correlation ( $-0.330$ ) between the chiasma frequency of the short bivalent and the combined chiasma frequencies of the long bivalents, on the basis of 36 pairs of observations. Table V A in FISHER's book gives the probability of such a correlation being significant as approximately 0.95.

The second method is more generally applicable. The variance is analysed into intra-cell (intra-class) and inter-cell (inter-class). If the former is significantly greater than the latter there is a negative correlation between the bivalents. It should be noted that this correla-

Non is an intra-class correlation whereas the former one was a inter-class correlation.

TABLE 2.

	Variance		$z$	Significance of $z$
	Intra-cell	Inter-cell		
<i>Secale</i> , plant 1 .....	0,4966	0,4975	0,0009	$z > 5\%$
» » 2 .....	0,3131	0,2584	0,1918	$z > 5\%$
» » 3 .....	0,4082	0,2226	0,3032	$5\% > z > 1\%$
» » 4 .....	0,6435	0,3782	0,2657	$5\% > z > 1\%$
» » 5 .....	0,5701	0,2192	0,4792	$1\% > z$
» » 6 .....	0,3061	0,1289	0,4323	$1\% > z$
» » 7 .....	0,5299	0,3499	0,2076	$5\% > z > 1\%$
» » 8 .....	0,5959	0,1553	0,6731	$1\% > z$
» » 9 .....	0,6270	0,3144	0,3452	$5\% > z > 1\%$
<i>Secale</i> , long chromosomes of DARLINGTON (1933) ...	0,5767	0,5955	0,0162	$z > 5\%$
<i>Vicia m</i> chromosomes ...	0,7080	0,3531	0,3478	$1\% > z$

In the last column  $z > 5\%$  means that the probability of this result occurring by random sampling from an uncorrelated population is greater than 0,05,  $5\% > z > 1\%$  means that the probability is between 0,05 and 0,01, and  $1\% > z$  that it is less than 0,01. These two points are FISHER's 5 % and 1 % points.

Table 1 gives the frequency distributions of chiasma formation in the bivalents and in the cells of nine plants of *Secale* with only the seven long bivalents, of the seven long bivalents of DARLINGTON's  $n=8$  rye, and of the five short ( $m$ ) bivalents of a plant of *Vicia faba*. Table 2 gives the results of the analyses of variance. In general the intra-cell variance is greater than the inter-cell variance. The  $z$  test of significance shows that in three of the rye plants (excluding DARLINGTON's case for the moment) the probability of the intra-class correlation being significant is greater than 0,99, in four cases it is between 0,95 and 0,99, and in the remaining two cases it is not significant. These results leave no doubt as to the existence of a negative intra-class correlation. It should be noted that any size differences will increase the intra-cell variance, but the small differences in seven chromosome rye cannot account for such an excess.

DARLINGTON's rye, as noted above, shows a negative inter-class correlation between the chiasma frequency of the small bivalent and the combined chiasma frequencies of the long ones. The analysis of

variance shows no signs of an intra-class correlation within the long ones (see Table 2).

The *Vicia* data are also open to both kinds of analysis. Table 3 gives the correlation table for the chiasma frequencies of the *M* and combined *m* bivalents. There is no significant inter-class correlation. On the other hand, Table 2 shows that there is a very significant intra-class correlation in the chiasma frequencies of the *m* bivalents. The probability of its significance is more than 0.99. This result coupled with the case of DARLINGTON's rye seems to indicate that, where there is a negative correlation, the short chromosomes will be affected more than the long ones. Proof of this point will, however, need more data.

TABLE 3. *Correlation table of the chiasma frequencies of the M and m bivalents in the pollen mother cells of Vicia faba.*

<i>M</i> bivalent		4	5	6	7	8	9	10	Total ( <i>m</i> )
<i>m</i> bivalents (sum)	13				1				1
	14					1			1
	15				1	1			2
	16			4	4	2			10
	17		1	4	7	5	1		18
	18		1	1	3	3	2	1	11
	19	1		3	1	1			6
	20				1				1
Total ( <i>M</i> )		1	2	12	18	13	3	1	

Correlation coefficient =  $-0.079$ . (Not significant.)

The occurrence of a negative correlation in both cross-over frequencies and chiasma frequencies of bivalents in various organisms adds yet another example to the number of cases in which crossing over and chiasma formation show markedly parallel behaviour. Apart from the evidence which leads to the conclusion that these two processes are somehow connected, for a summary of which see DARLINGTON (1932), we now have, in addition to the above, the following cases which indicate the relationship more precisely: —

1. The frequency distribution of the points of crossing over in the chromosomes of *Drosophila* is similar to that of the chiasmata in many organisms, both plant and animal (MATHER 1933).

2. The amount of non-disjunction, *i. e.* failure of pairing at first metaphase of meiosis, is inversely related to the frequency of crossing

over in the chromosomes of *Drosophila* (ANDERSON 1929, DOBZHANSKY 1932) as it is to chiasma formation in all the cases studied.

3. There is a correlation between the amount of crossing over in the chromosomes of a triploid female *Drosophila* and the disjunction of the chromosomes (RHOADES 1933). There is a similar correlation between chiasma formation and disjunction in trivalents (see MATHER 1934).

4. In *Zea-Euchlena* hybrids there is a corresponding reduction of crossing over and chiasma formation in a certain marked chromosome (BEADLE 1932). The amount of crossing over in this segment is almost precisely half the frequency of association.

5. In mice the male shows both less crossing over and a lower chiasma frequency than the female (CREW and KOLLER 1932).

6. The absence of visible crossing over in the male *Drosophila* is paralleled by special pairing properties of the chromosomes at meiosis (DARLINGTON 1934).

7. The frequency of chiasma formation in certain insects varies with temperature in precisely the same way as does the frequency of crossing-over in *Drosophila* (WHITE 1934).

Such results are predicted on the basis of the chiasmatype theory of chiasma formation and their occurrence must constitute very good evidence in favour of that theory. It is possible that they could be explained on the basis of non-chiasmatypy by surrounding the main hypothesis with a number of secondary ones, but they could not be predicted by that hypothesis.

Such evidence as this, when occurring so consistently in several cases all pointing the same way, is probably better support for the chiasmatype theory than the proofs of crossing over at individual chiasmata since it involves larger numbers of individuals in the observations.

A negative correlation of the frequencies of crossing over and chiasma formation in bivalents of the same cells presumably indicates a unitary, or at least partially unitary, control of these processes within the nucleus but we are not in a position to discuss the mechanism underlying these results, at the moment.

We are very much indebted to Dr. O. TEDIN for his help with the calculation of the statistics.

Sveriges Utsädesförening, Svalöf, June 1934.

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# ZUR GENETIK VON PHASEOLUS VULGARIS

## X. ÜBER INFLORESZENZTYPEN UND IHRE VERERBUNG

VON HERBERT LAMPRECHT

SAATZUCHTANSTALT WEIBULLSHOLM, LANDSKRONA

(With a summary in English)

ÜBER die Vererbung der bei *Phaseolus vulgaris* vorkommenden Infloreszenztypen liegen in der genetischen Literatur, soweit ich habe finden können, noch keine Mitteilungen vor. Dagegen ist die Stellung der Infloreszenzen im Verhältnis zur Achse mit Hinsicht auf ihre Vererbung von EMERSON (1904 und 1916) studiert worden. Bevor hier die Vererbung der untersuchten Infloreszenztypen besprochen wird, dürfte es angebracht erscheinen das Wichtigste über die Stellung der Infloreszenzen anzuführen, insbesondere da ich über einen neuen, bisher unbekannten Wuchstypus berichten kann, der eine Revision der Einteilung in Typen mit hoher und niedriger Achse angebracht erscheinen lässt.

EMERSON (l. c.) unterscheidet zwischen axialer und terminaler Infloreszenzstellung. Von diesen beiden soll die axiale Stellung für den rankenden, also hohen, die terminale für den nicht rankenden, also niedrigen Wuchstypus charakteristisch sein. EMERSON hat 1904 durch Kreuzungen nachgewiesen, dass die axiale über die terminale Infloreszenzstellung dominiert und dass es in solchen Kreuzungen zu einer monohybriden Aufspaltung nach dem Verhältnis 3 axial : 1 terminal kommt. Die gleiche Spaltung ist bereits von MENDEL (1865) konstatiert worden, nur unterschied MENDEL nicht zwischen axialer und terminaler Infloreszenzstellung, sondern zwischen hoher und kurzer Achse. Die beiden Varietäten — mit hoher bzw. kurzer Achse — wurden zur Zeit MENDELS als verschiedene Arten, *Phaseolus vulgaris* und *Ph. nanus*, aufgefasst.

Bei genauerem Zusehen findet man indessen bald, dass der Unterschied zwischen axialer und terminaler Stellung der Infloreszenzen keineswegs scharf ist, denn die sog. niedrigen Wuchsformen von *Phaseolus vulgaris*, die Buschbohnen, haben ausser den terminal stehenden Infloreszenzen auch unter diesen, in den unteren Blattachseln stehende

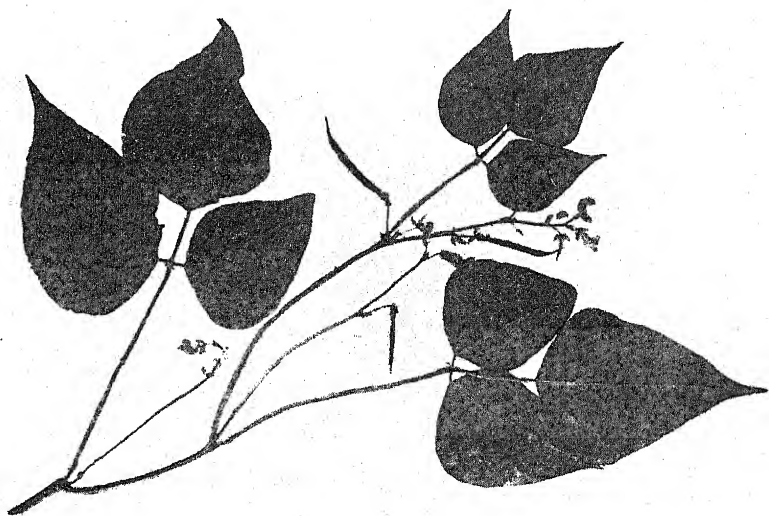


Fig. 1. Teil einer Buschbohnenpflanze. Der Stamm zeigt begrenztes Wachstum, trägt zwei axiale und endigt in eine terminale Infloreszenz.

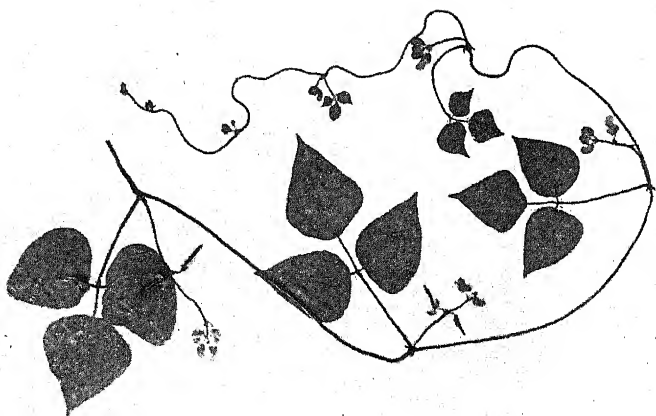


Fig. 2. Der oberste Teil einer hohen, rankenden Bohnenpflanze, bei der der Stamm unbegrenztes Wachstum und nur axiale Infloreszenzen aufweist.

axiale Infloreszenzen. Die Anzahl derartiger axialer Infloreszenzen, die vor der terminal auftretenden Infloreszenz an einem Stamme auftritt, variiert bei verschiedenen Biotypen. In Fig. 1 und 2 sind die beiden in Rede stehenden Typen abgebildet. Fig. 1 zeigt einen Teil einer Buschbohnenpflanze, bei der der Stamm zwei axiale und eine endständige (terminale) Infloreszenz trägt. Die unterste Infloreszenz ist die erste am Stamm von unten gerechnet auftretende. Fig. 2 zeigt einen Teil einer rankenden, hohen Bohnenpflanze, bei der der Stamm ausschliesslich axiale Infloreszenzen trägt. Es gibt demnach Typen mit nur axial stehenden und solche mit sowohl axial wie terminal stehenden Infloreszenzen. Es besteht also kein scharfer Trennungsgrund axiale : terminale Infloreszenzstellung, entsprechend hohem und niedrigem Wuchstypus.

Worin wir hier aber einen vollkommen scharfen Unterschied zu finden scheinen, das ist das unbegrenzte bzw. begrenzte Wachstum der Achse. Die von MENDEL (1865) gefundene Spaltung 3 hohe : 1 kurze Achse, bzw. die von EMERSON (1904) festgestellte Spaltung 3 axiale : 1 terminale Infloreszenzstellung wären also zu schreiben: 3 unbegrenztes Achsenwachstum : 1 begrenztes Achsenwachstum. Die Wahl dieses Einteilungsgrundes hat umso mehr Berechtigung an Stelle

der früher üblichen verwendet zu werden als in einer meiner Kreuzungen Pflanzen mit niedrigem Wuchs aufgetreten sind, die sehr kurze und zahlreiche, nicht rankende Internodien haben, bei denen aber die Achse unbegrenztes Wachstum aufweist.

In Fig. 3 ist eine derartige niedrige Bohnenpflanze mit unbegrenzt wachsender Achse abgebildet. Die Höhe dieser Pflanzen variierte in meinem Material zwischen 35 und 55 cm, während die Höhe verschiedener gewöhnlicher Buschbohrentypen mit begrenzt wachsender Achse zwischen 25 und 60 cm variierte. Die Internodienlänge der in

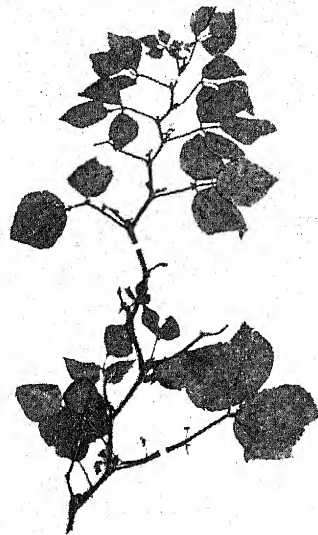
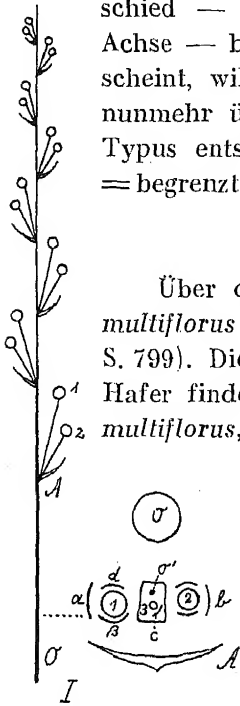


Fig. 3. Niedrige, ca. 45 cm hohe Bohnenpflanze mit unbegrenztem Wachstum des Stammes und sehr kurzen, in ausgesprochener Zickzackstellung wachsenden Internodien.



Fig. 3 abgebildeten Pflanze variiert zwischen etwa 2 und 4 cm. Der Stamm ist, wie ersichtlich, nicht rankend sondern steif aufrecht stehend. Die Internodien zeigen sog. Zickzackstellung, wodurch der Stamm in seinem Aussehen in hohem Grade an dasjenige von niedrigen *Pisum*-Pflanzen erinnert.

Da das Genpaar, das den in Rede stehenden phänotypischen Unterschied — unbegrenztes kontra begrenztes Wachstum der Achse — bedingt, bisher mit keinem Symbol belegt zu sein scheint, will ich hier die Gelegenheit benutzen es nach der nunmehr üblichen Weise — dem Charakter des rezessiven Typus entsprechend — mit *Fin*—*fin*, abgeleitet von *finitis* = begrenzt, zu bezeichnen.



Über den Bau der Infloreszenz von sowohl *Phaseolus multiflorus* wie *Ph. vulgaris* berichtet VELENOVSKÝ (1910, S. 799). Dieser schreibt: »Im Prinzip etwas ähnliches wie beim Hafer finden wir in der Infloreszenz der Fisoie (*Phaseolus multiflorus*, Fig. 490) vor«. (In Fig. 4 ist VELENOVSKÝs Fig. 490 I wiedergegeben). »Hier entspringen aus der Achsel der Blätter lange, aufrechte Trauben, welche jedoch in den Achseln der Hochblätter (A, B) immer zwei Blüten, eine ältere und eine jüngere, tragen. In welchem Verhältnisse befinden sich diese Blüten? An den Seiten beider sind kleine Schüppchen (a, b) zu sehen, welche den beiden erwähnten Blüten zur Stütze dienen.

Fig. 4. VELENOVSKÝs Fig. 490 I seiner Vergleichenden Morphologie der Pflanzen: »Zusammengesetzte Infloreszenz von *Phaseolus multiflorus* W.«. Erläuterung im Text.

In die Mitte beider Blüten ist ein drüsiges, vier-eckiges Gebilde eingekleilt, an welchem wir ein drittes, aber sehr verkümmertes Blütchen (3) erblicken, welches äusserlich ebenfalls durch ein kleines Schüppchen (c) unterstützt ist. Hinter diesem Blütchen befindet sich ein unbedeutender Höcker (o'). Wenn wir die Disposition der angedeuteten Bestandteile vergleichen, so können wir nicht daran zweifeln, dass die ganze Gruppe in der Achsel des Hochblattes (A) eine seitliche Traube vorstellt, deren Scheitel (o') und Blütchen (3) verkümmert ist und wo nur die ersten zwei Blüten zur Entwicklung gelangten. Bei der Species *Ph. vulgaris* pflegt nicht selten die mittlere Blüte ebenfalls entwickelt zu sein.»

Ob und in welcher Ausdehnung VELENOVSKÝs Auffassung des Infloreszenzbaues dieser beiden Arten als richtig angesehen werden kann, soll im folgenden untersucht werden. Seinen Ausführungen gemäss erscheint die Annahme berechtigt, dass die beiden Arten gleichen Infloreszenzbau besitzen.

In bezug auf *Phaseolus multiflorus* soll vor allem erwähnt werden, dass das zwischen den Ursprungsstellen der beiden Blütenstiele eingekellte viereckige Gebilde regelmässig vorhanden zu sein scheint. Auf diesem findet man auch stets ein knospenähnliches Gebilde mit Andeutung zu einem Schüppchen, das von VELENOVSKÝ als ein verkümmertes Blüthen (3) gedeutet worden ist. Der von VELENOVSKÝ erwähnte Höcker *o'* ist meistens sehr undeutlich, oft nicht sicher erkennbar. Eine Entwicklung des knospenähnlichen Gebildes zu einer dritten, mittleren Blüte habe ich bei *Ph. multiflorus* noch nicht auffinden können. Und auch VELENOVSKÝ hat über eine solche Entwicklung bei dieser Art nichts erwähnt.

Für *Ph. vulgaris* erwähnt VELENOVSKÝ indessen, dass »nicht selten die mittlere Blüte ebenfalls entwickelt zu sein« pflegt. Das bei *Ph. multiflorus* an der in Rede stehenden Stelle vorhandene viereckige Gebilde gleichwie auch der undeutliche Höcker *o'* scheinen aber — soweit ich bisher habe finden können — bei *Ph. vulgaris* nicht vorzukommen. Ich habe zusammen mehrere Hundert Individuen verschiedener Biotypen, auch aus Kreuzungen erhaltene, untersucht, und gleichfalls nicht selten eine mittlere, dritte, ja mitunter sogar noch eine vierte Blüte entwickelt gefunden. Aber die eben zitierte Angabe VELENOVSKÝs habe ich insofern nicht bestätigen können, als in allen Fällen — ob nun noch eine dritte oder sogar vier Blüten entwickelt gewesen sind — stets überdies das knospenähnliche Gebilde zwischen den Ursprungsstellen des ersten und zweiten Blütenstiels vorhanden gewesen ist. Und dieses ist bei *Ph. vulgaris* fast stets gut ausgebildet, 1—2 mm hoch.

Fig. 5 zeigt in Grundansicht vier Infloreszenzbilder von *Ph. vulgaris*. Das Nähere über diese dürfte sich ohne weiteres aus der Figuren-erklärung ergeben. Die unteren beiden Bilder zeigen deutlich die Lage einer eventuell entwickelten dritten und vierten Blüte. Keine dieser beiden entspricht der Lage des knospenähnlichen Gebildes II, das, wie wir später sehen werden, die Anlage zu einer Infloreszenzverzweigung darstellt. Die Blüten werden in ihrer Nummerfolge (1—4) entwickelt.

Hinsichtlich *Ph. vulgaris* fragt es sich nun, was das knospenähnliche Gebilde zwischen den Ursprungsstellen der Blütenstiele darstellt. Ist es wirklich als ein »sehr verkümmertes Blüthen« aufzufassen?, wie

es VELENOVSKÝ tut, wenn er sagt, dass bei dieser Art »nicht selten die mittlere Blüte ebenfalls entwickelt zu sein« pflegt. Diese Frage glaube ich mit recht grosser Sicherheit beantworten zu können; denn in meinem Bohnenmaterial besitze ich eine ganze Reihe von Biotypen, die zusammengesetzte Blütentrauben haben. Und an allen Punkten dieser Trauben, von denen seitliche Trauben entspringen, und zwar ganz gleichgültig ob man an diesen Stellen zwei, drei oder vier Blüten vorfindet, fehlt das erwähnte knospenähnliche Gebilde. Es dürfte daher

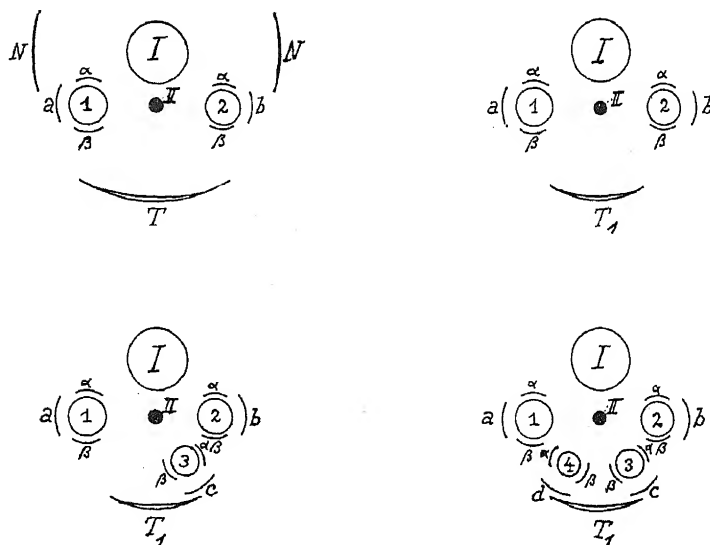


Fig. 5. Vier Grundansichten von Infloreszenzen von *Ph. vulgaris* L. Die Grundansicht links oben entspricht dem Ursprung der Infloreszenz in der Achsel des Tragblattes T; die übrigen drei Bilder zeigen Grundansichten, die den oberen Nodien der Infloreszenz entsprechen, und zwar mit 2, 3 bzw. 4 Blüten. I = Infloreszenzachse, II = Anlage zu einem Infloreszenzzweig, 1, 2, 3, 4 = Blüten, T = Tragblatt der Infloreszenz, N = Nebenblätter dieses, T<sub>1</sub> = Tragblättchen für einen Infloreszenzzweig, a, b, c, d = Stützblätter der Blüten, α, β = Vorblätter.

kaum zu bezweifeln sein, dass dieses die Anlage zu einer seitlichen Traube und nicht zu einer mittleren, dritten Blüte darstellt.

Nochmals soll hervorgehoben werden, dass bei *Ph. vulgaris* das viereckige Gebilde und der unbedeutende Höcker o' (siehe VELENOVSKÝ l. c.) stets zu fehlen scheinen. VELENOVSKÝ's Auffassung der Anlagen 3, c und o' seiner Fig. 490 der Infloreszenz von *Ph. multiflorus* könnte allerdings auch auf *Ph. vulgaris* bezogen werden, wenn man annähme, dass bei letzterer Art der Höcker o' zum knospenähnlichen Gebilde entwickelt sei und dass hier das »verkümmerte Blütchen« 3 und das kleine

Schüppchen *c* nicht zur Ausbildung gelangt sind. Diese Annahme würde jedoch mit VELENOVSKÝ'S Äusserung, dass bei *Ph. vulgaris* das Blütchen *3* nicht selten zu einer mittleren Blüte entwickelt ist, im Widerspruch stehen.

Es wäre denkbar, dass wir es hier mit einem bestimmten Unterschied zwischen *Ph. multiflorus* und *vulgaris* zu tun hätten. Aber über die Beschaffenheit der erwähnten Anlagen bei *Ph. multiflorus* wird allerdings erst dann Sicheres ausgesagt werden können, wenn diese einmal entwickelt angetroffen worden sind. Vielleicht wird es gelingen in Kreuzungen zwischen *Ph. multiflorus* und *vulgaris*, die ich im Gange habe, darauf eine Antwort zu erhalten.

In seinen Grundzügen dürfte der Bau der Infloreszenz von *Ph. vulgaris* durch das Vorstehende genügend charakterisiert worden sein. Im übrigen gibt es jedoch eine Anzahl verschiedener, zum grossen Teil erblich bedingter Infloreszenztypen. Die auftretenden Unterschiede beziehen sich auf die An- oder Abwesenheit von Infloreszenzverzweigungen, das Auftreten von akzessorischen Infloreszenzen, auf Anzahl und Länge der Internodien und auf die Anzahl von jedem Nodus entspringenden Blüten.

Die einfache, nicht verzweigte Infloreszenz repräsentiert den häufigsten Typus, der für die allermeisten Kulturrassen charakteristisch ist. Von diesem Haupttypus gibt es eine Reihe von Formen, von denen die wichtigsten in Fig. 6 dargestellt sind. Bei den einfachsten Formen, Fig. 6 *a*, *b* und *c*, entspringen von jedem Nodus der Infloreszenzachse stets nur zwei Blüten. Die Anzahl der Nodien variiert von 2 bis 7. Die Zahlen 6 und 7 sind jedoch nur selten anzutreffen. Die Anzahl Nodien ist erblich bedingt. Es gibt also Biotypen, bei denen in der Regel nur von 2 Nodien Blüten entspringen, solche mit 3 blütentragenden Nodien u. s. w. In gewissem, geringerem Masse wird die Anzahl der blütentragenden Nodien auch durch Milieufaktoren beeinflusst.

Bei der Angabe der Nodienanzahl wird der Ursprungspunkt der Infloreszenz in der Achsel des Tragblattes als erster Nodus gerechnet. Von diesem entspringen in der Regel auch Blüten; zuweilen — namentlich bei grösserer Nodienzahl — kann es vorkommen, dass die Blüten an dieser Stelle nur als Knospen vorhanden bleiben und sich nicht weiter entwickeln. Als oberster, letzter Nodus wird jener gerechnet, von dem aus noch normale Blüten entwickelt werden. Der stets vorhandene, kurze Fortsatz der Infloreszenzachse mit Knospen wird also nicht als Nodus gerechnet.

Anstatt zwei Blüten können von jedem Nodus drei oder vier ent-

springen. Siehe Fig. 6 *d* und *e*, sowie die frühere diesbezügliche Erörterung. Inwieweit diese Formen erblich bedingt sind kann noch nicht gesagt werden.

Im Habitus stärker abweichende Formen der unverzweigten Infloreszenz sind die mit akzessorischer Infloreszenz. Eine solche ist in Fig. 6 *f* schematisch dargestellt. Auch diese Formen können mit verschiedener Anzahl Nodien und verschiedener Anzahl Blüten per Nodus vorkommen. Man könnte vielleicht geneigt sein die Formen mit ak-

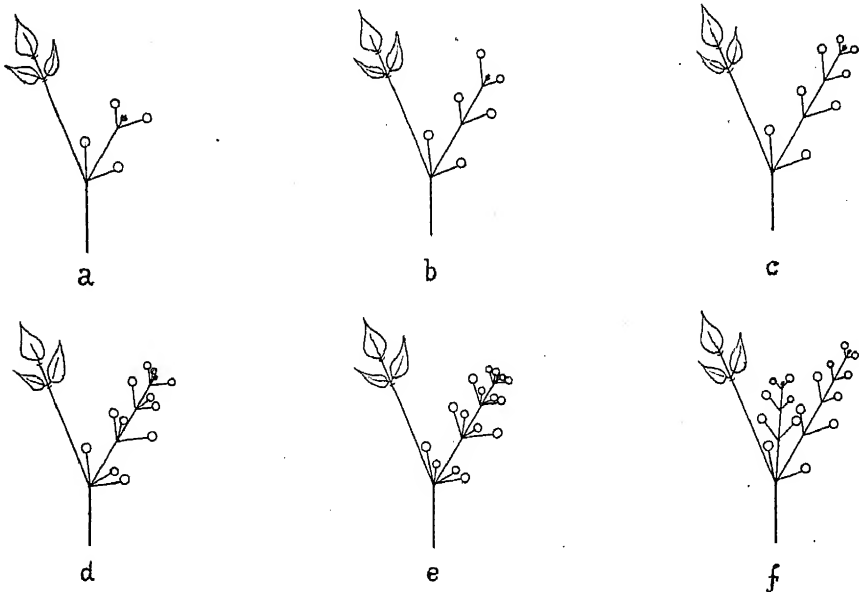


Fig. 6. Schematische Darstellung der wichtigsten Typen von unverzweigten Infloreszenzen von *Ph. vulgaris*. *a*, *b* und *c* unverzweigte, zweiblütige Infloreszenzen mit 2, 3 bzw. 4 Nodien; *d* und *e* unverzweigte Infloreszenzen mit drei bzw. vier Blüten von jedem Nodus; *f* unverzweigte, zweiblütige Infloreszenz mit akzessorischer solcher (Hauptinfloreszenz mit 5 Nodien).

zessorischen Infloreszenzen dem verzweigten Infloreszenztypus zuzurechnen, bei dem solchenfalls an den höheren Nodien keine Infloreszenz Zweige zur Ausbildung gekommen wären. Weiter unten bei der Besprechung der Kreuzungsergebnisse wird nachgewiesen werden, dass dies unrichtig wäre. Formen mit akzessorischen Infloreszenzen sind erblich gesehen dem unverzweigten Infloreszenztypus zuzurechnen. Fig. 7 zeigt eine ungewöhnliche, nicht verzweigte Form mit akzessorischer Infloreszenz. In der Achsel des Tragblattes gewahrt man eine ganz kurze akzessorische Infloreszenz mit 2 Hülisen. Die Hauptinfloreszenz ist dreiblütig. Am dritten Nodus derselben sieht man eine

seltene Erscheinung, zwei aus einer Blüte entwickelte Hülsen. Hierzu soll erwähnt werden, dass ich eine Linie, Nr. 31, besitze, bei der es nicht selten ist, dass in den Blüten zwei Fruchtblätter vorhanden sind. Gewöhnlich wird aber dann doch nur das eine dieser zu einer normalen Hülse entwickelt.

Beim zweiten bei *Ph. vulgaris* vorkommenden Infloreszenztypus ist die Infloreszenzachse verzweigt. Bei diesem haben wir es mit einer zusammengesetzten, und zwar mit einer homotaktischen Infloreszenz zu tun. Diese besteht aus einer Traube, bei der von den Nodien seitliche Trauben entspringen. Auch diese können wiederum Trauben tragen. Bisher habe ich einfache, zweifache und dreifache Verzweigung feststellen können. Drei solche Infloreszenzen sind in Fig. 8 a, b und c abgebildet. In Fig. 8 a sind die seitlichen Trauben ungewöhnlich schwach entwickelt. In Fig. 9 sind die genannten drei Verzweigungstypen, der Fig. 8 a, b und c entsprechend, schematisch dargestellt. Sie zeigen nur Stammteile und Tragblatt. Fig. 9 d zeigt den Stammtypus einer Form mit akzessorischer Infloreszenz.

Die verzweigten Infloreszenztypen von *Ph. vulgaris* sind erblich vollkommen festgelegt. Individuen mit verzweigten Infloreszenzen geben auch stets Nachkommen mit solchen Infloreszenzen. Die Ausbildung dieser Typen scheint von den Milieufaktoren praktisch genommen unabhängig zu sein.

Den verzweigten Infloreszenztypus habe ich unter Kulturformen von *Ph. vulgaris* bisher nur zweimal angetroffen. Die eine Sorte mit

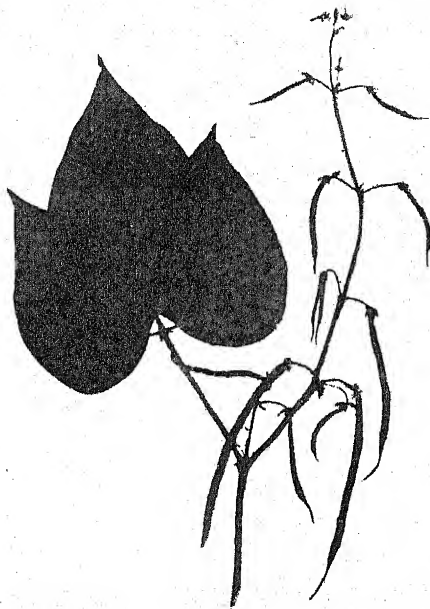


Fig. 7. Einfache, nicht verzweigte Infloreszenz von *Ph. vulgaris*. Dreiblütiger Typus; die dritte Hülse oder Blüte ist nicht immer zur Entwicklung gelangt. In der Achsel des Tragblattes entspringt eine kurze akzessorische Infloreszenz mit zwei Hülsen. Am dritten Infloreszenznodus sieht man links eine seltene Abnormität, 2 aus einer Blüte entwickelte Hülsen.

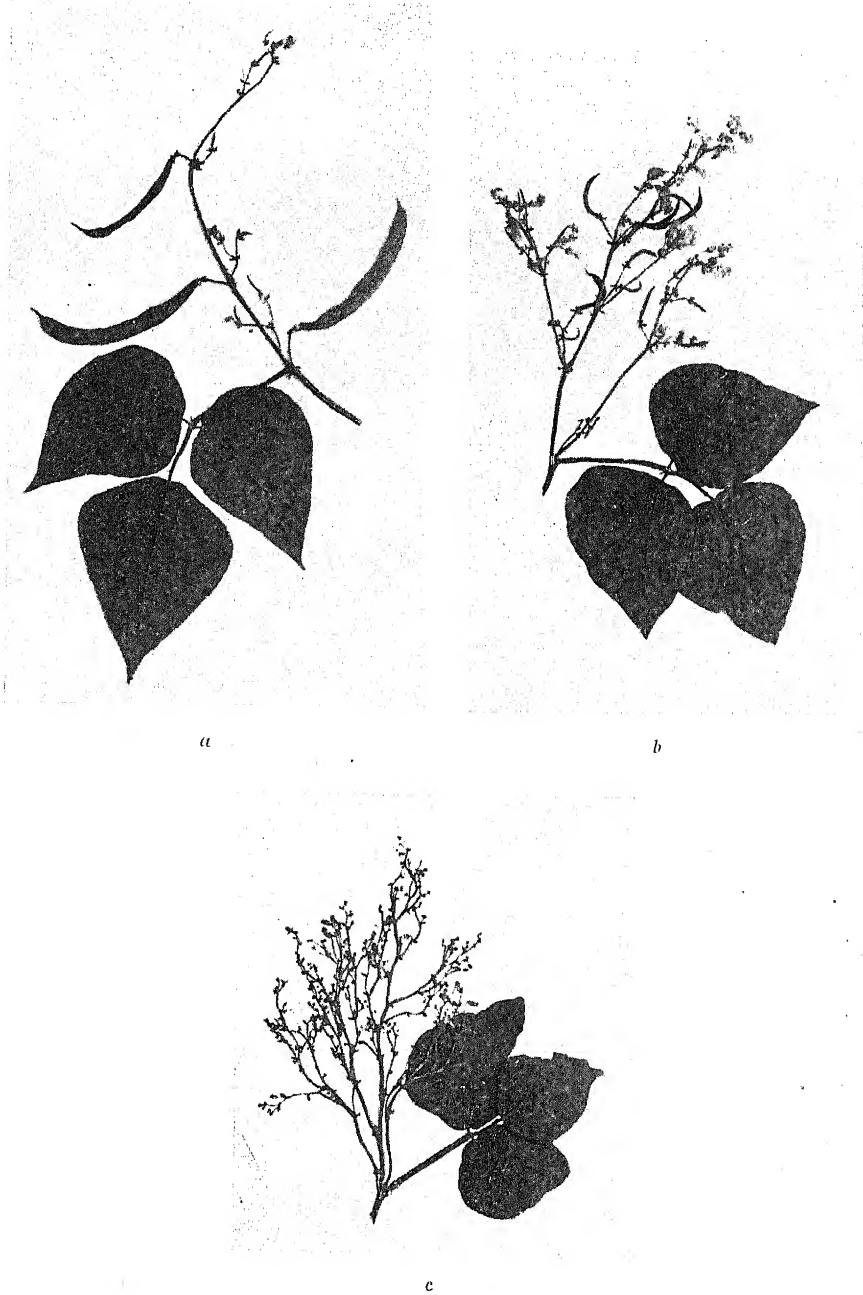


Fig. 8. Verzweigte Infloreszenzen von *Ph. vulgaris*. *a* Infloreszenz mit einfacher, schwach entwickelter Verzweigung, *b* mit zweifacher und *c* mit dreifacher Verzweigung.

diesem Typus ist *l'Inepuisable* von Vilmorin-Andrieux, Paris, die andere *New Abundance* von Webbs, Wordsley, England. *l'Inepuisable* ist bereits vor etlichen Jahren auf den Markt gekommen, *New Abundance*

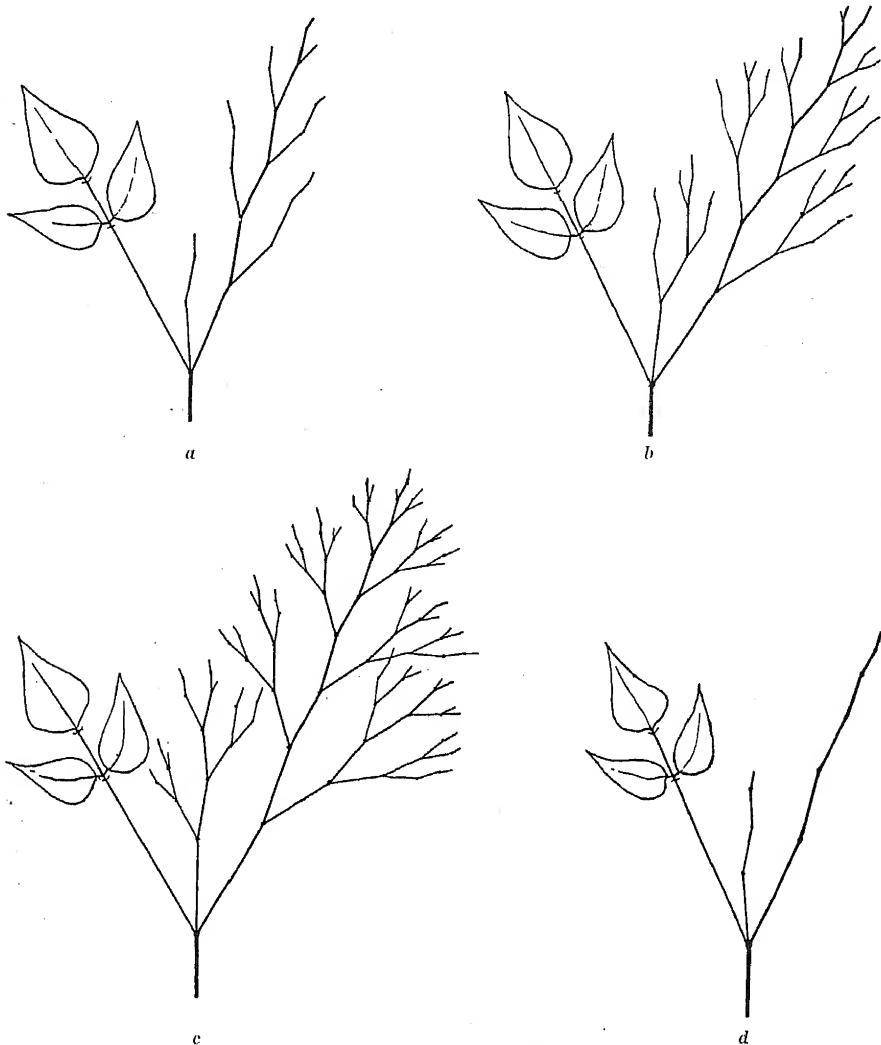


Fig. 9. Schematische Darstellung der Verzweigungstypen der in Fig. 7 abgebildeten Infloreszenzen (a, b und c) sowie einer einfachen, nicht verzweigten Infloreszenz mit akzessorischer solcher (d).

erst 1933. Diese beiden Sorten sind einander sehr ähnlich. Beide haben typisch zweifach verzweigte Infloreszenzen.

Zum Studium der Vererbung der verschiedenen Infloreszenztypen



wurden mehrere Kreuzungen mit einer Linie aus *l'Inepuisable*, L. 33, ausgeführt, von denen hier zwei, Kreuzung Nr. 18 und Nr. 23, näher besprochen werden sollen.

Kreuzung Nr. 18 wurde ausgeführt zwischen L. 35 aus der deutschen niedrigen Wachbohnsensorte *Hundert für Eine*, *Wachs* und L. 33. L. 35 hat einfache unverzweigte Infloreszenz mit durchschnittlich vier Nodien und zwei Blüten von jedem Nodus entspringend. Akzessorische Infloreszenzen habe ich nicht beobachtet. L. 33 hat wie erwähnt typisch zweifach verzweigte Infloreszenz, ferner eine Nodienanzahl von durchschnittlich 6—7 und gewöhnlich zwei, aber auch recht oft drei Blüten per Nodus. Bei L. 35 findet man zwischen den Ursprungsstellen der Blütenstiele stets das früher erwähnte knospenähnliche Gebilde, die Anlage zu einem Infloreszenzzweig, bei L. 35 dagegen fehlt dieses stets.

Die Pflanzen der ersten Generation hatten durchweg unverzweigte Infloreszenzen. Die Nodienanzahl der Infloreszenzen betrug 5—6, meistens 5, und von den Nodien entsprangen gewöhnlich zwei Blüten.

Die Individuen der zweiten Generation wurden, was die Infloreszenz betrifft, mit Hinsicht auf folgende Eigenschaften analysiert: Unverzweigte—verzweigte Infloreszenz, Vorhandensein akzessorischer Infloreszenzen, Anzahl Internodien per Infloreszenz, Anzahl Blüten per Nodus. Auf verschiedene Länge der Internodien wurde keine Rücksicht genommen. Auf die Anzahl Blüten per Nodus soll in dieser Arbeit nicht eingegangen werden. Im übrigen sind die Spaltungsergebnisse in Tabelle 1 zusammengestellt. In bezug auf die Nodienzahl sei erwähnt, dass stets die höchste an einem Individuum vorhandene vermerkt worden ist.

Die Ergebnisse in der ersten Generation zeigten, dass die unverzweigte Infloreszenz anscheinend vollkommen über die verzweigte dominiert. Die Nodienzahl der Infloreszenz war intermediär, für die Elternlinien war charakteristisch 4 bzw. 6—7, für die  $F_1$ -Pflanzen 5—6, meistens 5.

Die Spaltungsergebnisse in  $F_2$  (Tab. 1) zeigen, dass das Eigenschaftspaar unverzweigte—verzweigte Infloreszenz durch ein Genpaar bedingt wird. Wir finden monohybride Spaltung, und zwar:

Gefunden: 925 unverzweigte Infl. : 288 verzweigte Infl.

Erwartet: 909,75 » » : 303,25 » »

D/m für 3 : 1 = 1,01

Die erhaltenen Spaltungszahlen zeigen gute Übereinstimmung mit den theoretisch erwarteten. Das hier tätige Genpaar will ich mit dem Sym-

TABELLE 1.  $F_2$  der Kreuzung Nr. 18: *L. 33* aus *l'Inepuisable* (*ram ram*)  $\times$  *L. 35* aus *Hundert für eine Wachs* (*Ram Ram*).

Familien-Nr.	Individuen mit unverzweigten Infloreszenzen														Summe Individuen
	Ohne akzessorischen Infloreszenzen							Mit akzessorischen Infloreszenzen							
	Mit der Nodienzahl							Mit der Nodienzahl							
	2	3	4	5	6	7	2	3	4	5	6	7			
8009.....	2	22	29	14	1	—	—	2	3	2	1	—	—	77	
8010.....	3	18	25	12	2	1	—	—	4	—	—	—	—	65	
8011.....	3	24	14	8	3	—	—	1	2	3	—	—	—	58	
8012.....	3	23	19	7	—	—	—	2	1	—	—	—	—	55	
8013.....	3	32	23	5	1	—	—	—	1	1	—	—	—	66	
8014.....	3	17	17	12	1	1	—	—	1	2	—	—	—	54	
8015.....	4	32	19	6	3	—	—	1	1	2	—	—	—	68	
8016.....	3	22	26	11	—	—	—	—	—	1	—	—	—	63	
8017.....	6	24	23	8	—	—	—	—	2	—	—	—	—	63	
8018.....	8	36	13	7	1	—	—	1	1	1	—	—	—	68	
8019.....	5	22	24	7	1	—	—	—	2	—	—	—	—	61	
8020.....	3	26	18	4	1	—	—	—	1	1	—	—	—	54	
8021.....	6	19	21	9	—	—	—	—	1	2	—	—	—	58	
8022.....	5	27	20	6	—	—	—	—	2	—	—	—	—	60	
8023.....	3	17	27	8	—	—	—	—	—	—	—	—	—	55	
Summen:	60	361	318	125	14	2	—	7	22	15	1	—	—	925	

Familien-Nr.	Individuen mit verzweigten Infloreszenzen																		Summe Individuen
	Mit einfacher Verzweigung									Mit zweifacher Verzweigung									
	Mit der Nodienzahl									Mit der Nodienzahl									
	3	4	5	6	7	8	9	10	3	4	5	6	7	8	9	10	11		
8009.....	1	1	4	3	2	—	1	—	—	—	—	1	—	—	—	—	—	13	
8010.....	—	1	4	6	2	—	1	—	—	—	—	2	—	—	1	—	—	17	
8011.....	—	2	1	3	—	—	—	—	—	—	—	2	—	3	—	—	—	11	
8012.....	—	4	3	8	1	—	—	—	—	—	—	1	1	1	—	—	—	19	
8013.....	—	2	2	5	1	1	—	—	—	—	1	—	—	2	—	—	—	14	
8014.....	—	3	2	6	3	3	—	—	—	—	—	1	1	1	—	3	—	22	
8015.....	—	1	3	4	5	—	—	—	—	—	—	—	1	3	1	—	1	19	
8016.....	—	—	—	9	2	1	—	—	—	—	—	1	2	1	1	—	—	17	
8017.....	—	2	4	3	3	1	—	—	—	—	—	—	3	2	—	—	—	18	
8018.....	1	4	2	5	2	—	—	—	—	—	—	—	6	—	—	—	—	20	
8019.....	—	2	6	7	6	1	—	—	—	—	—	—	1	1	1	—	—	25	
8020.....	—	1	6	10	2	1	—	1	—	—	1	1	1	—	1	—	—	25	
8021.....	—	2	5	14	2	3	—	—	—	—	—	—	—	1	—	1	—	28	
8022.....	1	—	5	9	6	—	—	—	—	—	—	—	—	—	—	1	—	22	
8023.....	—	—	3	8	4	2	1	—	—	—	—	—	—	—	—	—	—	18	
Summen:	3	24	50	100	41	13	3	1	—	—	2	9	16	15	5	5	1	288	

bol *Ram*—*ram* bezeichnen, abgeleitet von *ramifera* = verzweigt, also der rezessiven Eigenschaft entsprechend.

Unter den 925 Individuen mit unverzweigter Infloreszenz finden wir 45 mit akzessorischer solcher. Die zweite Generation gestattet in bezug auf diesen Typus keine Schlusssätze hinsichtlich seiner Vererbung. Er wird bei der Besprechung der Spaltungsergebnisse in der dritten Generation abgehandelt werden.

In bezug auf die Zahl der Nodien per Infloreszenz ist aus Tabelle 1 zu entnehmen, dass sowohl bei den unverzweigten wie bei den verzweigten Typen eine recht grosse Variation derselben vorkommt. So variiert sie bei den ersteren zwischen 2 und 7, bei den letzteren zwischen 3 und 11. Unmittelbar ist in dieser Hinsicht aus Tabelle 1 ersichtlich, dass die Individuen mit verzweigter Infloreszenz eine erheblich höhere mittlere Nodienzahl haben müssen. Eine Berechnung der mittleren Nodienzahl für Individuen mit unverzweigten Infloreszenzen ergibt 3,66, für solche mit verzweigten Infloreszenzen 6,19.

Von einer Berechnung der mittleren Fehler dieser beiden Werte glaube ich Abstand nehmen zu können, da die Variationsgebiete der beiden Typen sich nur zu geringem Teile decken. Eine Vorstellung hiervon gibt Fig. 10, die die Frequenz der Nodienzahlen bei Individuen mit unverzweigter und verzweigter Infloreszenz, ausgedrückt in Prozenten, graphisch veranschaulicht. Wie aus dieser ersichtlich ist, überschneiden die beiden Kurven sich nur in etwa  $\frac{1}{5}$  des von ihnen im Ganzen eingenommenen Areal. Mit verzweigter Infloreszenz scheint demnach eine höhere Nodienzahl einherzugehen. Über die erbliche oder physiologische Bedingung dieser Erscheinung kann ich derzeit nichts Sicheres aussagen. Bisher ist es mir in  $F_3$  und  $F_4$  solcher Kreuzungen nicht gelungen bei unverzweigter Infloreszenz zu einer höheren Nodienzahl als 7 zu gelangen.

Aus Tabelle 1 ist ferner ersichtlich, dass eine Aufspaltung in Individuen mit einfacher und mit zweifacher Verzweigung der Infloreszenz stattgefunden hat. Die ersteren sind weitaus in der Mehrzahl. Es wurden gefunden 235 mit einfacher Verzweigung und 53 mit zweifacher. Das Verhältnis entspricht nicht gut einem monohybriden. Zu erwarten wäre 216 einfache : 72 zweifache. D/m beträgt hierfür 2,58. Die einfache Verzweigung scheint in dieser Kreuzung jedoch sicher über die zweifache zu dominieren.

Die Nodienzahl ist bei zweifacher Verzweigung der Infloreszenz deutlich grösser als bei einfacher. Als Mittelwerte wurden in dieser Kreuzung gefunden: 5,85 für einfache und 7,59 für zweifache Verzwei-

gung. Dieser Unterschied ist — gleichwie die entsprechenden Zahlen für unverzweigt—verzweigt — statistisch sicher.

Die Vererbungsweise der akzessorischen Infloreszenz sowie der eventuelle Zusammenhang der Nodienzahl mit Homo- und Heterozygotie im Genpaar *Ram*—*ram* sollen gemeinsam mit den Ergebnissen der

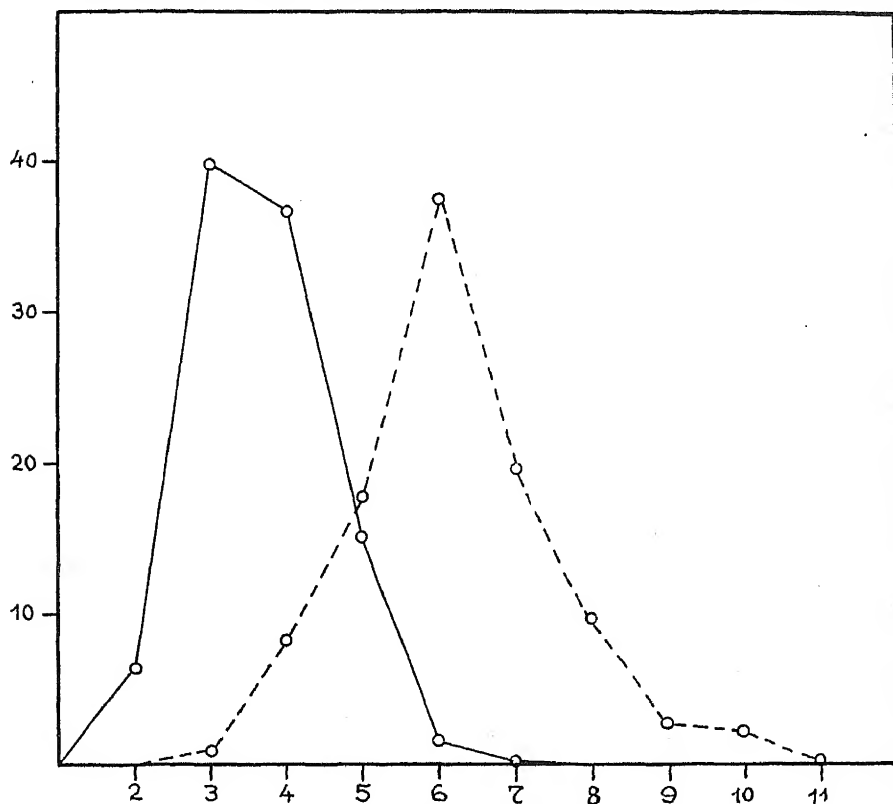


Fig. 10. Die Frequenz der Nodienzahlen bei Individuen mit unverzweigten (——) und verzweigten Infloreszenzen (- - - -) in  $F_2$  der Kreuzung Nr. 18. Abszisse = Nodienzahl, Ordinate = Frequenz in Prozenten.

dritten Generation von sowohl Kreuzung Nr. 18 wie Nr. 23 abgehandelt werden.

Kreuzung Nr. 23 wurde ausgeführt zwischen L. 4 aus *Saxonia* und L. 33 aus *l'Inepuisable*. L. 4 hat einfache unverzweigte Infloreszenz mit durchschnittlich nur drei Nodien und zwei Blüten von jedem Nodus entspringend. Akzessorische Infloreszenzen habe ich nicht beobachtet. In bezug auf L. 33 siehe oben. Hinsichtlich das knospenähnliche Gebilde gilt das für L. 35 Gesagte.

Auch in dieser Kreuzung hatten die Pflanzen der ersten Generation durchweg unverzweigte Infloreszenzen. Die Nodienzahl der Infloreszenzen betrug gleichwie in Kreuzung Nr. 18 5—6, meistens 5, und von den Nodien entsprangen gewöhnlich zwei Blüten.

Die Analyse der  $F_2$ -Individuen erfolgte in jeder Hinsicht wie schon für Kreuzung Nr. 18 erwähnt worden ist. Für Kreuzung Nr. 23 sind die Spaltungsergebnisse in Tabelle 2 zusammengestellt. Auch in dieser

TABELLE 2.  $F_2$  der Kreuzung Nr. 23: *L. 4 aus Saxonia (Ram Ram) × L. 33 aus l'Inepuisable (ram ram)*.

Familien-Nr.	Individuen mit unverzweigten Infloreszenzen															Summe Indivi- duen
	Ohne akzessorischen Infloreszenzen							Mit akzessorischen Infloreszenzen								
	Mit der Nodienzahl							Mit der Nodienzahl								
	2	3	4	5	6	7	8	2	3	4	5	6	7	8		
8081.....	2	7	10	9	3	1	—	—	—	—	—	—	—	—	32	
8082.....	1	7	17	15	10	3	—	—	—	—	—	—	1	—	54	
8083.....	—	9	21	8	7	3	1	—	—	—	1	—	—	—	50	
8084.....	—	4	11	18	5	3	—	—	—	—	1	—	—	—	42	
8085.....	1	3	15	27	17	4	—	—	—	1	—	—	—	—	68	
8086.....	—	4	11	13	9	7	—	—	—	—	—	—	1	—	44	
8087.....	—	8	15	11	3	2	1	—	—	—	—	—	—	—	41	
8088.....	—	8	16	12	5	1	1	—	—	—	—	—	—	—	43	
8089.....	—	6	6	10	6	3	—	—	—	—	1	—	—	—	32	
8090.....	1	10	5	8	6	3	—	—	—	—	—	—	—	—	33	
8091.....	2	4	15	20	18	2	—	—	—	1	—	—	—	—	62	
8092.....	1	4	12	16	9	2	—	—	—	—	—	—	—	—	44	
8093.....	1	4	17	26	17	3	—	—	—	—	2	—	—	—	70	
8094.....	1	5	13	14	12	4	—	—	—	—	—	—	—	—	49	
8095.....	2	2	4	1	3	—	1	—	—	—	—	—	—	—	13	
8096.....	—	2	13	10	4	1	—	—	—	—	—	—	—	—	30	
8097.....	—	2	6	6	2	2	—	—	—	—	—	2	—	—	20	
8098.....	1	2	11	10	6	2	1	—	—	—	—	—	1	—	34	
8099.....	—	1	4	6	6	4	1	—	—	—	—	—	—	—	22	
8100.....	1	3	5	4	5	—	2	—	—	—	—	—	—	—	20	
8101.....	1	13	13	18	16	3	—	—	—	—	—	—	—	—	64	
8102.....	2	10	11	23	11	4	—	—	—	—	—	—	—	—	60	
8103.....	4	2	12	6	1	—	—	—	—	—	—	—	—	—	25	
8104.....	—	7	12	6	3	—	—	—	—	—	—	—	—	—	28	
8105.....	4	7	19	20	5	1	—	—	—	—	—	—	—	—	56	
8106.....	1	4	12	11	7	—	—	—	—	—	—	1	—	—	35	
8107.....	1	8	16	20	9	6	—	—	—	—	—	—	—	—	60	
Summen:	27	146	322	348	203	64	8	—	—	2	5	3	3	—	1131	

Familien-Nr.	Individuen mit verzweigten Infloreszenzen															Summe Indivi- duen						
	Mit 1-facher Ver- zweigung					Mit 2-facher Ver- zweigung					Mit 3-facher Verzweigung											
	Mit der Nodien- zahl					Mit der Nodien- zahl					Mit der Nodien- zahl											
	3	4	5	6	7	8	9	4	5	6	7	8	9	10	11		6	7	8	9	10	11
8081.....	—	—	—	2	—	—	—	—	—	1	5	1	—	1	1	—	—	—	—	—	—	11
8082.....	—	—	—	1	3	—	—	—	—	1	3	4	7	1	—	—	—	—	—	—	—	20
8083.....	—	—	—	—	—	—	—	1	5	4	5	2	—	—	—	—	—	—	—	—	—	17
8084.....	—	—	2	—	—	—	—	—	—	3	3	—	1	—	—	—	1	—	—	—	—	10
8085.....	—	—	1	—	1	—	—	—	—	2	8	4	—	3	—	—	—	—	—	—	—	19
8086.....	—	—	1	—	—	—	—	—	—	1	2	7	6	—	—	—	—	—	—	—	—	17
8087.....	—	—	—	—	—	—	—	—	—	1	—	1	3	—	—	—	—	—	—	—	—	5
8088.....	—	—	—	—	—	—	—	1	—	6	2	1	1	—	—	—	—	—	1	2	—	14
8089.....	—	—	—	—	—	—	—	—	—	1	8	4	1	1	—	—	—	—	—	—	—	15
8090.....	1	—	—	1	—	—	—	—	—	—	3	7	1	—	—	—	—	—	—	—	—	13
8091.....	—	—	1	1	1	1	—	—	—	1	4	1	4	—	—	—	—	—	1	—	—	14
8092.....	—	—	—	1	1	1	—	—	1	1	4	6	3	—	1	—	—	1	—	1	—	21
8093.....	—	—	—	—	—	—	—	—	—	1	2	6	4	2	—	—	—	—	—	—	—	15
8094.....	—	—	2	—	—	—	—	—	—	—	1	3	1	—	—	—	—	—	—	—	—	7
8095.....	—	—	—	1	—	—	—	—	—	1	1	5	—	—	—	—	—	—	—	1	—	9
8096.....	—	—	—	—	—	—	—	—	1	1	1	3	2	—	—	—	—	—	—	—	—	8
8097.....	—	—	—	—	—	1	—	—	1	—	4	5	1	1	1	—	—	—	—	—	—	14
8098.....	—	—	—	—	—	—	—	—	—	—	3	5	1	—	—	—	—	1	—	—	—	10
8099.....	—	—	1	—	1	—	—	1	—	1	1	5	4	—	—	—	—	—	—	1	—	15
8100.....	—	—	—	—	—	—	—	—	—	—	1	3	5	1	—	—	—	—	—	—	—	11
8101.....	—	—	—	—	—	—	—	—	—	1	3	7	3	—	—	—	—	—	1	—	—	15
8102.....	—	—	—	3	1	—	—	—	1	2	1	2	4	—	—	—	—	—	—	—	—	14
8103.....	—	—	—	—	—	—	—	—	1	1	4	2	—	—	—	—	—	—	—	—	—	8
8104.....	—	—	—	—	7	—	—	—	—	—	—	—	1	—	—	—	—	—	—	—	—	2
8105.....	—	—	1	2	—	—	—	—	—	1	6	7	4	—	—	—	—	—	—	—	—	21
8106.....	—	—	—	2	2	1	—	—	1	—	3	4	2	—	—	—	—	1	—	—	—	16
8107.....	—	—	1	—	1	—	—	—	—	—	3	—	—	—	—	—	—	—	—	—	—	5
Summen:	1	—	10	14	12	3	—	1	6	26	84	100	61	11	3	—	1	3	3	5	—	346

Kreuzung wurde vollkommene Dominanz der unverzweigten über die verzweigte Infloreszenz festgestellt. Ferner war auch die Nodienzahl in  $F_1$  eine intermediäre.

Für die Aufspaltung im Genpaar *Ram*—*ram* erhalten wir in  $F_2$  folgende Zahlen:

Gefunden: 1131 unverzweigte Infl. : 346 verzweigte Infl.

Erwartet: 1107,<sup>75</sup> » » : 369,<sup>25</sup> » » »

D/m für 3 : 1 = 1,<sup>40</sup>

Auch in dieser Kreuzung kann gute Übereinstimmung mit dem monohybriden Spaltungsverhältnis 3 : 1 konstatiert werden. Erwähnt verdient vielleicht zu werden, dass in beiden Kreuzungen ein geringes Defizit an Individuen mit verzweigten Infloreszenzen vorkommt.

In  $F_2$  dieser Kreuzung sind, wie Tab. 2 zeigt, Individuen mit sowohl ein-, zwei- wie auch dreifach verzweigten Infloreszenzen aufgetreten. Überraschend ist, dass hier die Individuen mit zweifacher Infloreszenzverzweigung weitaus in der Mehrzahl sind. Hinsichtlich des erblichen Verhaltens dieser beiden Gruppen zueinander kann ich vorläufig nichts Sicheres aussagen. Vielleicht handelt es sich hier um eine Modifikation von zwei- zu einfach verzweigten Infloreszenzen. Untersuchungen in weiteren Generationen werden hier Klarheit schaffen müssen. Nur in bezug auf den Typus mit dreifacher Verzweigung der Infloreszenz hat in  $F_3$  und  $F_4$  festgestellt werden können, dass er konstant rein erhalten werden kann und gegenüber den ein- und zweifach verzweigten Typen rezessiv ist. Für das hierfür verantwortliche Genpaar schlage ich die Bezeichnung *Iter—iter*, abgeleitet von der rezessiven Eigenschaft *iteratus—ramifera* = wiederholt verzweigt, vor.

In Kreuzung Nr. 23 wurde eine viel geringere Anzahl Individuen mit akzessorischen Infloreszenzen gefunden als in Kreuzung Nr. 18, nämlich nur 13 unter 1131 Individuen mit unverzweigten Infloreszenzen. Um eine eventuelle genotypische Bedingtheit des Auftretens von akzessorischen Infloreszenzen festzustellen, wurden die Samen von 11 solchen  $F_2$ -Individuen in  $F_3$  ausgesät. Zehn von den erhaltenen Familien zeigten Spaltung im Genpaar *Ram—ram*, und die hierbei erhaltenen Resultate sind in Tab. 3 zusammengestellt.

Aus Tab. 3 geht hervor, dass keines der  $F_2$ -Individuen mit akzessorischen Infloreszenzen ausschliesslich oder auch nur eine nennenswerte Anzahl Nachkommen mit solchen Infloreszenzen gegeben hat. Im Gegenteil, in 5 Familien sind überhaupt keine solchen Individuen aufgetreten, und Gleiches gilt für die im *Ram—ram*-Genpaar nicht spaltende Familie. Im ganzen wurden in  $F_3$  141 Individuen mit unverzweigten Infloreszenzen erhalten, und unter diesen sind 5 mit akzessorischen Infloreszenzen aufgetreten. Ähnliches wurde in  $F_3$  der Kreuzung Nr. 18 gefunden. Hier traten unter 323 Individuen nur 5 mit akzessorischen Infloreszenzen auf. Man kann demnach mit grosser Sicherheit behaupten, dass die Ausbildung einer akzessorischen Infloreszenz in den vorliegenden Kreuzungen nicht durch ein besonderes Genpaar bedingt wird, sondern wahrscheinlich modifikativ verursacht wird.

Die Individuen mit akzessorischen Infloreszenzen sind also hier jenen mit unverzweigten Infloreszenzen zuzurechnen.

Schliesslich soll das Genpaar *Ram—ram* in seinem Verhältnis zum Auftreten einer verschiedenen Anzahl von Nodien in der Infloreszenz untersucht werden. In  $F_1$  beider Kreuzungen hat festgestellt werden können, dass die Nodienzahl, verglichen mit der der beiden Eltern, intermediär gewesen ist. Zur Klarlegung dieser Verhältnisse, wie auch zu rein praktischen Züchtungszwecken, wurden von den beiden Kreu-

TABELLE 3. Die Spaltung von Individuen mit unverzweigter und gleichzeitig akzessorischer Infloreszenz in  $F_3$  der Kreuzung Nr. 23.

Familien-Nr.	Individuen mit nur unverzweig- ter Inflores- zenz	Individuen mit unverzweigter und akzesso- rischer Inflo- reszenz	Individuen mit verzweigter Infloreszenz	Summe Individuen
4463 .....	11	2	6	19
4464 .....	12	1	7	20
4466 .....	17	—	3	20
4467 .....	15	—	2	17
4468 .....	13	1	5	19
4469 .....	14	1	4	19
4470 .....	13	—	7	20
4471 .....	13	—	5	18
4472 .....	11	—	8	19
Summen:	119	5	47	171
	124			
Erwartet.....	128,25		42,75	
D/m für 3:1 =	0,75			

zungen mehrere Tausend Individuen in  $F_3$  untersucht. Hier wird nur der für die vorliegenden Fragen wesentliche Teil mitgeteilt.

Vorweg soll erwähnt werden, dass die Spaltungen in  $F_3$  die auf Grund der  $F_2$ -Ergebnisse angenommene Wirkung des Genpaares *Ram—ram* durchaus bestätigen. Sämtliche Individuen mit verzweigten Infloreszenzen, die *ram—ram*-Individuen, haben in  $F_3$  wiederum ausschliesslich *ram—ram*-Individuen gegeben. In Kreuzung Nr. 23 wurden 952 Individuen diesbezüglich untersucht. Die Individuen mit unverzweigten Infloreszenzen (ohne akzessorischen solchen) haben teils im Genpaar *Ram—ram* Spaltung gezeigt, teils haben sie konstant unverzweigte Nachkommen gegeben. Im ganzen wurden diesbezüglich



69 Familien untersucht. Diese haben folgende Spaltungsresultate gegeben.

Gefunden: 49 spaltende : 20 konstante Familien

Erwartet: 46 » : 23 » »

D/m für 2 : 1 = 0,77

Für die spaltenden Familien wurde erhalten:

Gefunden: 1054 unverzweigte Infl. : 323 verzweigte Infl.

Erwartet: 1032,75 » : 344,25 » »

D/m für 3 : 1 = 1,32

Die gefundenen Spaltungszahlen zeigen gute Übereinstimmung mit den theoretisch erwarteten an, aber auch hier wurde, gleichwie in den beiden  $F_2$ -Generationen, ein kleines Defizit an Individuen mit verzweigten Infloreszenzen gefunden. Und Gleiches gilt für  $F_3$  von Kreuzung Nr. 18, nämlich:

Gefunden: 323 unverzweigte Infl. : 92 verzweigte Infl.

Erwartet: 311,25 » : 103,75 » »

D/m für 3 : 1 = 1,33

Bei Vereinigung der Resultate in beiden Kreuzungen und Generationen erhält man folgende Zahlen:

Gefunden: Kreuzung 18 $F_2$ :	925	unverzweigte Infl. :	288	verzweigte Infl.	
» 18 $F_3$ :	323	» : 92	»	»	
» 23 $F_2$ :	1131	» : 346	»	»	
» 23 $F_3$ :	1054	» : 323	»	»	
Zusammen:	3433	» : 1049	»	»	
Erwartet:	3361,5	» : 1120,5	»	»	
D/m für 3 : 1 =	2,46				

Das erwähnte Defizit tritt also hier schon viel deutlicher zutage und es fragt sich, ob wir es hier nicht mit einer geringen Elimination von *ram—ram*-Individuen zu tun haben.

Mit Hinsicht auf das Verhalten der Nodienzahl der Infloreszenzen zum Genpaar *Ram—ram* ist bereits früher festgestellt worden, dass *ram—ram*-Individuen eine durchschnittlich viel grössere Nodienzahl aufweisen als *Ram—Ram*- und *Ram—ram*-Individuen zusammen. Wie verhält sich nun die Nodienzahl bei dominanter Homo- und bei Heterozygotie im Genpaar *Ram—ram*? Zur exakten Klarlegung dieser Frage wurde eine grössere Anzahl  $F_3$ -Individuen nach  $F_2$ -Individuen mit bekannter Nodienzahl gebaut und analysiert.

In Kreuzung Nr. 18 wurden hierbei folgende Resultate erhalten. Bei 10  $F_2$ -Pflanzen mit der Konstitution *Ram—Ram* variierte die Nodien-

zahl von 2—4. Der Mittelwert betrug  $3,50 \pm 0,213$ . Bei 15 *Ram—ram*-Individuen, die also in  $F_3$  spalteten, variierte die Nodienzahl von 3—7 und der Mittelwert betrug  $4,60 \pm 0,253$ . Eine Berechnung ergibt, dass der Unterschied zwischen den erwähnten beiden Mittelwerten für die Nodienzahlen der *Ram—Ram*- und *Ram—ram*-Individuen statistisch sicher ist.  $m_{\text{Diff.}}$  beträgt 0,331 und  $D/m_{\text{Diff.}} = 3,33$ .

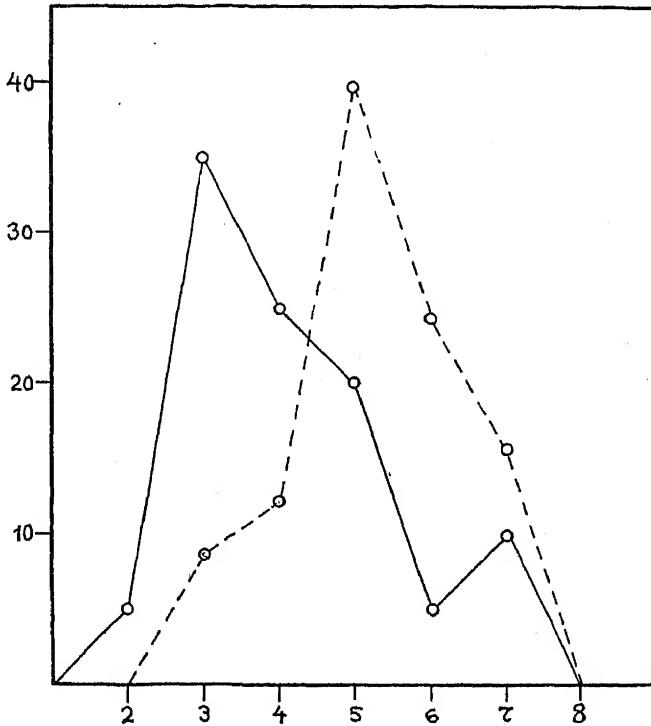


Fig. 11. Die Frequenz der Nodienzahlen bei *Ram Ram*- (—) und *Ram ram*-Individuen (---) in  $F_2$  der Kreuzung Nr. 23. Abzisse = Nodienzahl, Ordinate = Frequenz in Prozenten.

Für Kreuzung Nr. 23 wurden diesbezüglich folgende Resultate erhalten. 20  $F_2$ -*Ram—Ram*-Pflanzen ergaben als Mittelwert für die Nodienzahl der Infloreszenzen  $4,15 \pm 0,298$ . Der entsprechende Mittelwert für 58 *Ram—ram*-Individuen betrug  $5,26 \pm 0,147$ . Auch hier ist der Unterschied zwischen den beiden Mittelwerten als statistisch sicher zu betrachten, da die Differenz deutlich nennenswert mehr als das Dreifache des mittleren Fehlers derselben erreicht.  $m_{\text{Diff.}} = 0,333$  und  $D/m_{\text{Diff.}}$  erreicht 3,34. In Fig. 11 ist die Frequenz der Nodienzahlen für

*Ram—Ram-* und *Ram—ram*-Individuen, ausgedrückt in Prozenten, graphisch dargestellt. Auch die Kurven illustrieren, wie ersichtlich, deutlich den Unterschied in erwähnter Hinsicht.

Schliesslich wurde der Mittelwert für 46 *ram—ram*-Individuen der Kreuzung Nr. 23, die in  $F_3$  untersucht worden sind, ermittelt und mit dem entsprechenden Wert für die oben angeführten 58 *Ram—ram*-Individuen verglichen. Für erstere wurde erhalten  $7,93 \pm 0,208$ , für letztere  $5,26 \pm 0,147$ .  $m_{\text{Diff}}$  beträgt 0,255 und  $D/m_{\text{Diff}}$  10,45. Zwischen *ram—ram*- und *Ram—ram*-Individuen finden wir demnach für die Nodienzahl der Infloreszenzen einen viel grösseren Unterschied als zwischen den *Ram—Ram-* und *Ram—ram*-Individuen. Im letzteren Falle erreichte  $D/m_{\text{Diff}}$  für Kreuzung Nr. 18 3,33 und für Kreuzung Nr. 23 3,34. Heterozygotie im Genpaar *Ram—ram* verursachte also nicht vollkommen intermediäre Nodienzahl der Infloreszenzen, sondern diese Zahl nähert sich sehr deutlich derjenigen der *Ram—Ram*-Individuen. Die Wirkung dieses Genpaares auf die Nodienzahl ist wahrscheinlich so aufzufassen, dass sie die durch andere, bisher nicht analysierte Gene bestimmte Nodienzahl modifiziert.

### SUMMARY.

1. In the introduction the author points out the inappropriate use hitherto of the character pairs tall — low mode of growth and axial — terminal inflorescences as an expression for a definite pair of genes. The tall forms exhibit an unlimitedly growing stem, but such stems are also found among low forms (v. Fig. 3). Tall forms have always only axial inflorescences, low forms may have terminal and axial or only axial. The author therefore suggests the use of the always univocal difference, stem with unlimited or limited growth and recommends the designation *Fin—fin*, derived from *finitis* = limited, for the pair of genes in question.

2. In the same manner as VELENOVSKÝ (1910) the ground-plan of the inflorescence of *Phaseolus vulgaris* has been subjected to a close study, when it was ascertained that the bud-like formation between the original sites of the flower stems is the rudiment of a lateral branch of the inflorescence and not, as VELENOVSKÝ asserts, a stunted, undeveloped central third flower. In proof of this evidence is produced to show that this formation is always missing when lateral branchings of the inflorescence have been developed, whereas it is always found when a third flower occurs without the simultaneous occurrence of inflorescent branchings.

3. The type of inflorescence occurring in *Ph. vulgaris* has been studied with respect to the absence and presence of inflorescent branchings, the occurrence of accessory inflorescences, the number of nodes and the number of flowers developing from each node.

4. The inheritance of the characters enumerated in paragraph 3 has been studied in two crosses in  $F_2$  and  $F_3$ . It appears that the character-pair, absence—presence of inflorescent branchings, is conditioned by a single pair of genes, which are designated *Ram*—*ram*, derived from *ramifera* = branch-bearing, corresponding to the recessive form. Complete dominance seems to prevail: *Ram*—*Ram* and *Ram*—*ram* individuals have always unbranched inflorescences.

5. Three types of inflorescent ramifications are established, single, double and treble. The three-fold ramified inflorescence (Figs. 8 c and 9 c) is recessive in relation to the other two. The pair of genes responsible for this are designated by the symbol *Iter*—*iter*, derived from *iteratus*—*ramifera* = repeatedly branched.

6. The occurrence of individuals with accessory inflorescences was shown not to be due to a special pair of genes. The development of such ramifications seems to be modificatorily conditioned. The progeny of individuals with accessory inflorescences exhibit the same composition as the progeny of individuals without such inflorescences. In both cases a small percentage of individuals appear with accessory branchings.

7. Between ramified inflorescences and the number of inflorescent nodes there is a very high degree of positive correlation. Further, it was ascertained that *Ram*—*ram* individuals exhibit a greater number of nodes than *Ram*—*Ram* individuals. The difference in this respect is statistically significant.

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# EINE PISUM-FORM MIT COMPACTUM- VERZWEIGUNG UND VERKÜRZTEN STAUBFÄDEN

VON HERBERT LAMPRECHT

SAATZUCHTANSTALT WEIBULLSHOLM, LANDSKRONA

(With a summary in English)

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IM Jahre 1932 beobachtete ich in der dritten Generation einer Kreuzung zwischen der dänischen Markerbsensorte Hamlet und der aus England stammenden Markerbse Witham Wonder in sechs Familien das Auftreten von eigentümlich missbildeten Pflanzen. Diese Beobachtung wurde damals erst an den bereits im Reifen begriffenen Erbsenpflanzen gemacht.

Die in Rede stehenden Pflanzen waren in diesem Jahre gewöhnlich ein wenig niedriger als die übrigen und zeigten in den meisten Blattachseln an Stelle der Infloreszenzen sehr kompakte Stammverzweigungen. Das kompakte Aussehen beruhte teils darauf, dass diese Stammverzweigungen sehr kurze Internodien hatten, teils darauf, dass in den Blattachseln dieser Verzweigungen meistens nicht Infloreszenzen sondern wiederum Stammverzweigungen mit sehr kurzen Internodien sich entwickelten. Die kompakten Stammverzweigungen erreichten gewöhnlich nur eine zwischen 7 und 15 cm variierende Gesamtlänge. Ausserdem konnte beobachtet werden, dass die allermeisten Knospen dieser Pflanzen, die auf den Stammverzweigungen auftraten, nicht oder kaum zum Aufblühen gelangten und dass sich aus ihnen auch keine Hülsen entwickelten. Nur ab und zu konnte an einer Pflanze eine solche aufgefunden werden. Das Ganze machte den Eindruck, dass die Fertilität in irgendeiner Weise gestört sei und dass im Zusammenhang hiermit eine wiederholte Verzweigung in den Blattachseln stattfände.

Die Pflanzen der sechs erwähnten Familien wurden in bezug auf normale und solche mit kompakten Stammverzweigungen klassifiziert und ausgezählt. Es waren insgesamt 609 Individuen, von denen 462 als normal, 138 als *compactum* und 9 als zweifelhaft *compactum* bezeichnet wurden. Die Klassifikation der Pflanzen war demnach in diesem Jahre keine ganz sichere. Aber die Zahlen sprechen doch mit

recht grosser Wahrscheinlichkeit für eine monohybride Spaltung im Verhältnis 3 normale : 1 *compactum*-Pflanzen. Rechnet man die 9 zweifelhaften *compactum*-Individuen zur *compactum*-Gruppe so resultiert:

Gefunden: 462 normal : 147 *compactum*

Erwartet: 456,75 » : 152,25 »

D/m für 3 : 1 = 0,50

Von den typischen *compactum*-Pflanzen konnten in diesem Jahre keine keimfähigen Samen erhalten werden. Im übrigen wurden natürlich sämtliche Pflanzen gesondert geerntet um die Vererbungsweise dieses Typus sicher feststellen zu können.

Im Jahre 1933 wurden von 30 Pflanzen je 30 Samen ausgesät. Von den erhaltenen 30 Familien haben 26 in normale und *compactum*-Pflanzen aufgespaltet, 4 haben nur normale Nachkommen gegeben. Bei monohybrider Spaltung wäre zu erwarten gewesen: 20 spaltende : 10 konstante Familien. D/m erreicht für dieses Verhältnis (2 : 1) den Wert von 2,32. Die Übereinstimmung ist also nicht gut, aber bei Verursachung der Spaltung durch ein Genpaar noch sehr wohl möglich.

In diesem Jahre (1933) wurden sämtliche Pflanzen genau auf die Häufigkeit und Ausbildung von *compactum*-Verzweigungen sowie auf den Grad von Fertilität, der Anzahl ausgebildeter Hülsen und Samen untersucht.

Der Typus einer *compactum*-Pflanze ist in Fig. 1 abgebildet. Von der in der Fig. 1 abgebildeten Pflanze sind der besseren Übersicht halber zwei gleich unten am Stamm entspringende Verzweigungen entfernt worden. An vier aufeinander folgenden Blattachsen — von unten gerechnet — sieht man *compactum*-Zweige entspringen. Der vierte Zweig ist am kräftigsten entwickelt. Die *compactum*-Verzweigungen machen hier durchweg den Eindruck von aus kleinen Blättern, Ranken und Knospen bestehenden Knäueln. Die Einzelheiten sind schwer oder kaum zu unterscheiden. Die *compactum*-Verzweigungen von der fünften bis zur achten Blattachse liegen teils auf der Rückseite der Pflanze, teils sind sie von Blättern mehr oder weniger verdeckt. An der neunten Blattachse entspringt eine Hülse von anscheinend normaler Grösse. Diese Hülse enthält, wie vielleicht auch in der Figur wahrnehmbar ist, nur drei Samen. Die Samenanlagen sind demnach wahrscheinlich nur teilweise befruchtet worden. Hierzu sei erwähnt, dass die beiden Elternsorten der Kreuzung sowie auch die Nachkommen derselben sonst im allgemeinen eine hohe Zahl Samen pro Hülse aufweisen, etwa 6—10.

Die auf der *compactum*-Pflanze ausgebildete Hülse unterscheidet

sich indessen auch in einer anderen Hinsicht von den Hülsen sonstiger Pflanzen der genannten Kreuzung. Ihr Stiel ist ungewöhnlich kurz, seine Länge beträgt 1—1,5 cm. Bei den anderen Pflanzen variiert seine Länge gewöhnlich zwischen 3—5 cm. Diese Erscheinung hat für alle bisher an *compactum*-Pflanzen gefundenen Hülsen festgestellt werden können.

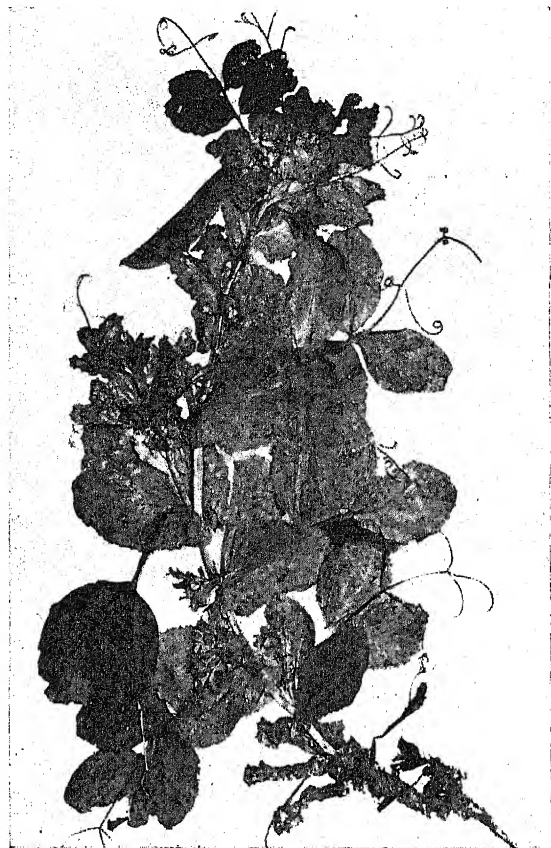


Fig. 1. Teil einer Erbsenpflanze mit *compactum*-Verzweigungen.

In Fig. 2 ist ein *Pisum*-Blatt mit in der Achsel desselben entspringender *compactum*-Verzweigung abgebildet. Damit das Bild an Klarheit gewinnt, wurden von der *compactum*-Verzweigung einige sekundäre Zweige entfernt. Wie ersichtlich sind die Internodien der Verzweigung sehr kurz; ihre Länge variiert — abgesehen vom ersten mit einer Länge von 3—5 cm — zwischen 0,5 und 1,5 cm. In der ersten, zweiten und dritten Blattachsel des *compactum*-Zweiges entspringen

sekundäre solche Zweige (bei den oberen sind diese entfernt), deren Internodienlänge noch kürzer ist. Erst auf diesen sekundären Zweigen sind unbedeutende Knospen zur Entwicklung gelangt.

Die Blätter der *compactum*-Verzweigungen zeigen die übliche Gestalt mit Blättchen und Ranken, nur sind sie eben erheblich kleiner als die des Hauptstammes der Pflanze.

Wie oben erwähnt worden ist, sind 1933 die *compactum*-Pflanzen in bezug auf den Grad der Fertilität und die mehr oder weniger extreme Ausbildung der *compactum*-Zweige genau untersucht worden. Von einer Wiedergabe der diesbezüglichen Details glaube ich Abstand neh-

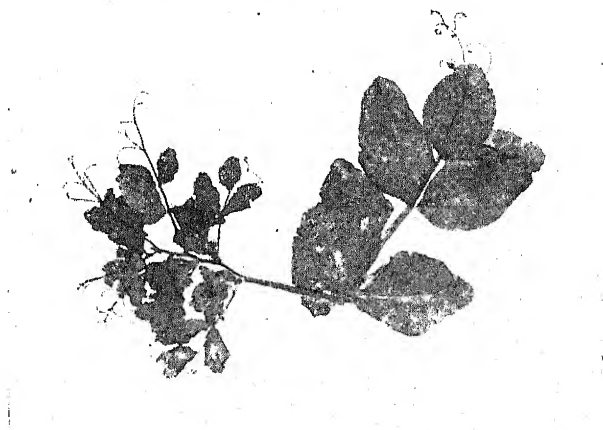


Fig. 2. Ein *Pisum*-Blatt mit in der Achsel desselben entspringender *compactum*-Verzweigung.

men zu können, da in diesen Hinsichten keine sicher verschiedenen Typen gefunden werden konnten. Es waren alle Übergänge vorhanden. Mit normalen Pflanzen konnten die *compactum*-Pflanzen jedoch kaum verwechselt werden. Eine Analyse der Spaltung hat zu den in Tabelle 1 mitgeteilten Ergebnissen geführt.

Die Resultate sprechen zweifellos für eine monohybride Spaltung: 3 ohne : 1 mit *compactum*-Verzweigung.

Im Jahre 1933 war der Ansatz von Hülsen ein viel grösserer als 1932. In diesem Jahre wurden, wie schon früher erwähnt, keine keimfähigen, sondern nur 2—3 untaugliche Samen an *compactum*-Pflanzen erhalten. 1933 haben unter den 135 *compactum*-Pflanzen wenigstens 20 1—3 Hülsen mit allerdings gewöhnlich nur 1—2 Samen ausgebildet.



Die höchste gefundene Samenzahl pro Hülse war 5. Worauf diese Erscheinung zurückzuführen sein könnte, verblieb auch 1933 — da leider keine Untersuchung von Androeceum und Gynoeceum erfolgt war — ungeklärt.

TABELLE 1. Die Spaltung normale : *compactum* Pflanzen in 26 Familien im Jahre 1933.

Familien-Nr.	Anzahl Individuen		Familien-Nr.	Anzahl Individuen	
	Phänotypisch normale	<i>compactum</i>		Phänotypisch normale	<i>compactum</i>
6888	16	7	6902	18	5
6889	13	6	6904	24	3
6890	15	6	6905	13	2
6891	12	6	6906	16	4
6892	25	3	6908	18	5
6893	15	7	6909	18	4
6894	20	4	6910	17	8
6895	14	9	6911	25	2
6896	15	11	6912	13	4
6897	14	9	6913	23	6
6898	17	6	6915	26	3
6899	10	3	6916	14	3
6900	19	1	6917	22	8
Summen:	205	78	—	247	57
Transport:	247	57	—	—	—
Total	452	135			
Erwartet:	440,25	146,75			
D/m für 3:1 = 1,12					

Im Jahre 1934 wurden Samen von 33 normalen, aus spaltenden Familien stammenden Pflanzen, sowie von 9 typischen *compactum*-Pflanzen, ausgesät. Bevor an die Beurteilung der Pflanzen geschritten wurde, wurden Androeceum und Gynoeceum untersucht, wobei sich folgendes ergab.

Im Androeceum waren wie gewöhnlich neun Staubblätter verwachsen, das zehnte frei. Die Staubfäden waren jedoch in ihrem freien, nicht verwachsenen Teil erheblich kürzer als wie bei normalen Pflanzen. Und dasselbe gilt für das zehnte, freie Staubblatt. In Fig. 3 sind Androeceum und Gynoeceum dargestellt. Wie aus der Figur hervorgeht, trifft die Verkürzung nicht alle Staubfäden im gleichen Masse. Die mittleren sind am stärksten verkürzt, die seitlichen am wenigstens.

Die ersteren erreichen kaum ein Drittel der normalen Länge, die letzteren etwa die Hälfte.

Das Gynoeceum zeigt im grossen normale Gestalt. Jedoch ist das Fruchtblatt in den meisten Fällen mit seinen Rändern nur unvollständig verwachsen. Die Anzahl und das Aussehen der Samenanlagen sind normal.

Die eben besprochenen Verhältnisse im Androeceum und Gynoeceum sind an sämtlichen 1934 ausgespaltenen *compactum*-Pflanzen und an etwa gleichviel normalen Pflanzen untersucht worden. Durchweg hat festgestellt werden können, dass die erwähnten Erscheinungen stets für *compactum*-Pflanzen charakteristisch sind, an normalen aber

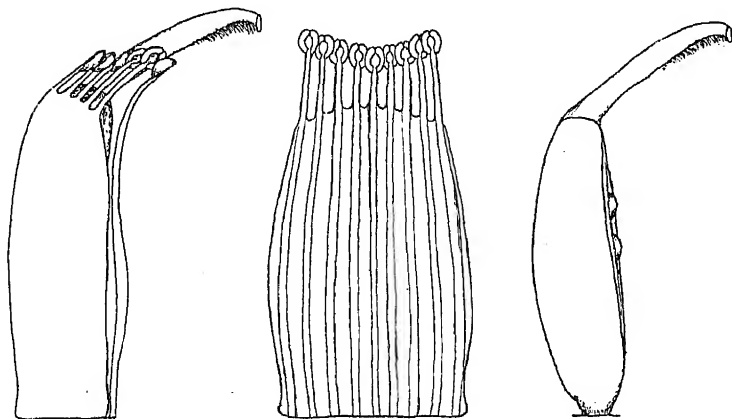


Fig. 3. Androeceum und Gynoeceum einer *Pisum*-Pflanze mit *compactum*-Verzweigung. Die Staubfäden sind in ihrem freien Teil stark verkürzt, das Fruchtblatt ist nur teilweise verwachsen.

niemals vorgekommen sind. Von 15 *compactum*-Pflanzen sind ausserdem Pollenproben mikroskopisch untersucht worden. Der Pollen ist offenbar ganz normal; bei Vergleich mit Pollen von normalen Pflanzen hat sich kein Unterschied ergeben. Alle Körner zeigten reichen Inhalt, die bekannte orangegelbe Farbe und hatten gewöhnliche Grösse.

Die Spaltungszahlen von 1934 sind in Tabelle 2 zusammengestellt. Wie aus dieser hervorgeht, konnte das Resultat von 1933 bestätigt werden, es besteht deutlich monohybride Spaltung laut dem Verhältnisse 3 phänotypisch normale Pflanzen : 1 mit *compactum*-Verzweigung und verkürzten Staubfäden. Das Genpaar, das dieser Spaltung zugrundeliegt, will ich mit dem Symbol *Brev*—*brev* bezeichnen, abgeleitet von *brevifilamentosus* = mit kurzen Staubfäden, als der typischsten, stets scharf umgrenzten Eigenschaft.

TABELLE 2. Die Spaltung normale : *brevifilamentosus*—*compactum* Pflanzen in 16 Familien im Jahre 1934.

Familien-Nr.	Anzahl Individuen		Familien-Nr.	Anzahl Individuen	
	Phänotypisch normale	<i>brevifila- mentosus- compactum</i>		Phänotypisch normale	<i>brevifila- mentosus- compactum</i>
3577	25	4	3596	2	1
3578	20	8	3598	20	8
3579	14	5	3605	6	3
3588	21	5	3611	8	2
3591	24	2	3613	3	1
3592	17	6	3072	34	5
3593	21	5	3074	29	9
3594	6	3	3077	25	11
Summen:	148	38	—	127	40
Transport:	127	40	—	—	—
Total:	275	78			
Erwartet:	264,75	88,25			
D/m für 3 : 1 = 1,26					

Es ist wohl kaum anzunehmen, dass es sich hier nur um ein Genpaar handelt. Es wäre eigentümlich, wenn dasselbe Genpaar für zwei so stark verschiedene Eigenschaften wie verkürzte Staubfäden und *compactum*-Verzweigungen des Stammes allein verantwortlich wäre. Wahrscheinlich handelt es sich um eine Komplexmutation von zwei stark gekoppelten Genen. Gleiches dürfte übrigens auch für das Genpaar *Uni—uni* Gültigkeit haben, das bei *Pisum* einfache Blätter, wiederholt verzweigte Infloreszenzen und pistiloid umgebildete Blütenelemente verursachen sollte (siehe LAMPRECHT, 1933). Auf eine ähnliche Erscheinung hoffe ich binnen kurzem bei *Phaseolus vulgaris* zurückkommen zu können.

Für das Verhältnis der spaltenden zu den nicht spaltenden Familien wurden 1934 folgende Zahlen erhalten.

Gefunden: 16 spaltende : 17 nicht spaltende Familien

Erwartet: 22 » : 11 » » »

D/m für 2 : 1 = 2,21

Bei Vereinigung der 1933 und 1934 erhaltenen Zahlen resultiert:

Gefunden: 42 spaltende Familien : 21 konstante Familien. Also genau das theoretisch erwartete Verhältnis.

Aus den Samen, die 1933 von 9 *compactum*-Pflanzen geerntet und

1934 ausgesät wurden, haben sich nur wiederum *compactum*-, also *brev—brev*-Pflanzen entwickelt. In letzterem Jahre war der Hülse-ansatz an *brev—brev*-Pflanzen noch grösser als 1933. Auch war die Anzahl der pro Hülse erhaltenen Samen bedeutend grösser, vielleicht das doppelte von 1933 erreichend. Worauf ist dieses stark variierende Auftreten von Hülse und der stark verschiedene Prozent von Samen-ansatz in verschiedenen Jahren zurückzuführen?

Zweifellos dürfte sein, dass eine Selbstbefruchtung in der Knospe infolge der stark verkürzten Staubfäden unmöglich ist. Der Pollen kann von den geplatzten Staubbeuteln nicht von selbst auf die gut 2 mm höher gelegene Narbe hinaufgelangen. Man vergleiche Fig. 3. Ich glaube nicht fehlzugehen, wenn ich das Zustandekommen von Befruchtungen mit dem Auftreten von Blasenfüssen, *Thrips*, in Zusammenhang bringe. Zwischen dem Auftreten dieser Tiere und der Frequenz von Hülse-ansatz und Samenansatz besteht nämlich für die drei Jahre 1932, 1933 und 1934 sicherlich eine gute positive Korrelation. 1932 sind Blasenfüsse nur sehr wenig aufgetreten, 1933 in bedeutend grösserer Anzahl und 1934 schliesslich, während des aussergewöhnlich warmen und trockenen Sommers in sehr grosser Anzahl. Zur Übertragung von Pollen auf die Narbe sind sowohl die Larven wie die Imagines dieser Tiere gut geeignet.

Schliesslich sei erwähnt, dass in den Blattachsen von *brev—brev*-Pflanzen, in denen Hülse zur Entwicklung gelangen, eine *compactum*-Verzweigung nicht oder nur in geringem Umfange anzutreffen ist. Man bekommt hier den Eindruck, als ob die eingetretene Befruchtung und damit die beginnende Entwicklung der Hülse die weitere Entwicklung einer *compactum*-Verzweigung inhibiere.

### SUMMARY.

1. In  $F_3$  of a cross between two varieties of marrow peas, Hamlet and Wilham Wonder, the author gives evidence of the segregation in 6 families of abnormal plants with compact branching in the leaf-axes.

2. The *compactum* plants (see Figs. 1 and 2) were for the most part sterile. But in different years a highly varying percentage of pods was developed. An examination of the plants and an analysis of the segregation of abnormal plants during two years show the following: —

3. All *compactum* plants have also greatly shortened filaments (v. Fig. 3), which renders self-fertilization impossible.

4. The cause of the small number of pods always produced,

although there is a wide variation in the number, is explained by the author as the result of *Thrips* in the flower-buds. Larvae as well as Imagines are capable of conveying pollen. Between the appearance of *Thrips* and the production of pods during the years 1932, 1933 and 1934 there is a good positive correlation.

5. The ascertained segregation normal : *compactum* plants is typically monohybrid, a fact also confirmed by the ratio between the number of segregating and constant families.

6. The pair of genes underlying the segregation is designated by the author by the symbol *Brev--brev*, derived from *brevifilamentosus* = with short filaments.

7. The author is of opinion that this is a case of a complex mutation of two closely linked genes.

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# CYTO-GENETIC STUDIES ON HYBRIDS BETWEEN TWO PHLEUM SPECIES

BY ARNE MÜNTZING

SVALÖF, SWEDEN

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## I. INTRODUCTION.

IN the autumn of 1931 the somatic chromosome numbers of a series of timothy types were determined in the chromosome laboratory of the Svalöf Plant Breeding Institute. Under the helpful guidance of Dr. NILS SYLVÉN and Dr. G. NILSSON-LEISSNER the plants were selected from the cultures of the Forage Crop Department. Besides specimens of ordinary timothy, *Phleum pratense* L. this collection comprised plants of *Phleum nodosum* L., *P. alpinum* L., *P. Boehmeri* WIB. and *P. Michelii* ALL.

With the exception of *P. Michelii* the chromosome numbers of these species are already known. *P. pratense* has  $2n=42$  and is hexaploid, as the basic number of the genus is seven (AVDULOW 1928, according to TISCHLER 1931, GREGOR and SANSOME 1930, AVDULOW 1931). *P. nodosum* L., which is synonymous to the »*Phleum pratense* Group II» described by GREGOR and SANSOME, is diploid ( $2n=14$ , GREGOR and SANSOME 1930). *P. Boehmeri* has the same number (AVDULOW 1928, according to TISCHLER 1931). In *P. alpinum*, finally, GREGOR and SANSOME (l. c.) found that biotypes from Scotland were tetraploid ( $2n=28$ ), whereas a strain obtained from Sweden had only 14 chromosomes.

Our own chromosome counts gave the following result: Nineteen different biotypes of *P. nodosum* (Swedish origin), one biotype of *P. Boehmeri* and one of *P. Michelii* had all  $2n=14$ . In *P. alpinum* two biotypes from north Sweden (Pajala and Pello) were tetraploid ( $2n=28$ ), a third biotype from Switzerland however proved to be diploid ( $2n=14$ ). Of the 26 *pratense* types studied 21, as expected, had  $2n=42$  or  $\pm 42$ , but 5 other plants, which morphologically belonged to *pratense*, had a somewhat lower number, 35 or 36. This was quite surprising and therefore the chromosome numbers of those five plants were again controlled by new fixations and repeated counts. The reexamination, however, confirmed the preliminary result. Of the five plants two had  $2n=35$ , two  $2n=36$ , the remaining plant had either 35 or 36 chromosomes.

As those plants were pentaploid or approximately pentaploid it was concluded that they were hybrids of some kind. Studies of their ancestry and progeny have verified this assumption and demonstrate that the plants are derivatives from spontaneous hybrids between *P. pratense* and *P. nodosum*.

The ancestry of the hybrids cannot be reconstructed in detail, but the following data may be mentioned. Four of the five plants were found in a progeny obtained after open pollination from the plant »900». The fifth plant was a daughter of plant »950», which had been pollinated with pollen from »900». The plants »950» and »900» had unfortunately been discarded, but according to the records of the Forage Crop Department they descended from two original plants, »578» and »386» respectively. Both these plants were still alive, and their chromosome numbers could be determined. Plant »578» proved to be hexaploid and a typical *pratense*, whereas plant »386», the original mother of plant »900», was diploid ( $2n = 14$ ) and morphologically of the *nodosum* type. The latter plant was descended from a *P. pratense* f. *stoloniferum* obtained from the Botanical Garden of Stockholm. According to ASCHERSON and GRAEBNER *P. pratense* f. *stoloniferum* is a form of *P. nodosum* (cf. WITTE 1915, p. 150).

There are many generations between the original *nodosum* plant and the pentaploid hybrids. These generations were raised partly after isolation, partly after open pollination of the mother individuals. Under such circumstances it is impossible to reconstruct in detail how the plants with 35—36 chromosomes have arisen. However, as no other *Phleum* species than *nodosum* and *pratense* were cultivated at Svalöf at the same time as the diploid mother plant and its descendants, it is highly probable that the observed 35- and 36-chromosome plants are descendants from spontaneous hybrids between *nodosum* and *pratense*. On account of their chromosome number they cannot be primary hybrids but are probably products of back-crosses between the primary hybrids and *Phleum pratense* (cf. discussion below).

*P. pratense* is a quite polymorphic species (cf. WITTE 1912, 1915) and the morphological differences between *pratense* and *nodosum* are quantitative rather than qualitative (cf. GREGOR 1931, p. 211). Therefore the hybrid plants, detected by chromosome counts, can not be distinguished from pure *pratense*. Their *nodosum* ancestry is indicated only by a somewhat decumbent mode of growth, but in any case, they are much more similar to *pratense* than to *nodosum*. (Figs. 30—32.)

The hybrids were partially sterile but had a remarkably high

percentage of apparently good pollen grains. This percentage was examined in three of the hybrids which had been divided vegetatively into a number of clone plants. The average values of 13, 14 and 7 samples respectively were 82.1, 85.1 and 81.8 per cent good pollen. The first and second means are from 36 chromosome plants, the third one from a hybrid with 35 chromosomes. Three pollen samples from pure *pratense* gave the values 91, 95 and 100 per cent, and two samples from *nodosum* contained 84 and 95 per cent good pollen grains. Consequently, pollen fertility is probably somewhat lower in the hybrids than in the pure species.

There is also a decrease in fertility on the female side. After open pollination the same hybrids in which pollen fertility had been studied had 23, 44 and 31 seeds resp. per cm. of the panicle. Each value is based on counts from 3—5 clone plants. A normal *pratense* biotype, growing close to the hybrids, had the corresponding value 83 (average of 6 clone plants). According to SYLVÉN (1929) the number of seeds per cm. of the panicle after open pollination is rather different in different biotypes of *pratense* and in different years. However, the average values of 29 normal *pratense* biotypes listed in table 1 (l. c. pp. 3—5) were calculated and found to be  $74.2 \pm 4.6$ .

When isolated the hybrids set seed rather poorly but in part this is probably due to selfsterility of the same kind as is characteristic of most *pratense* biotypes (cf. SYLVÉN 1929, VALLE 1931). — In the spring of 1932, however, seeds harvested from isolated clone plants of the hybrids were received from the Forage Crop Department. Those seeds were germinated and gave a new generation,  $I_1$ . Before discussing morphology, fertility and chromosome conditions in this generation an account of the meiotic behaviour in the mother plants will be given.

## II. STUDIES ON MEIOSIS IN THE HYBRIDS.

In order to study meiosis in the pollen mother cells spikelets were fixed in diluted chromacetic formalin with prefixation in Carnoy. The paraffin sections were stained with gentian violet.

Three hybrids, mother plants of three  $I_1$ -families, were studied. Of those plants two had 36 and one 35 chromosomes. The best slides were obtained from one of the 36-chromosome plants, in which the main course of the meiotic divisions is the following.

At I—M, observed in side view, a variable number of univalents were more or less separated from the metaphase plate and easy to



distinguish. The number of such univalents was counted in 100 p. m. c. The following frequency was obtained:

Number of univalents: ...	1	2	3	4	5	6	n	M $\pm$ m
Frequency: .....	4	16	29	31	17	3	100	3.50 $\pm$ 0.12

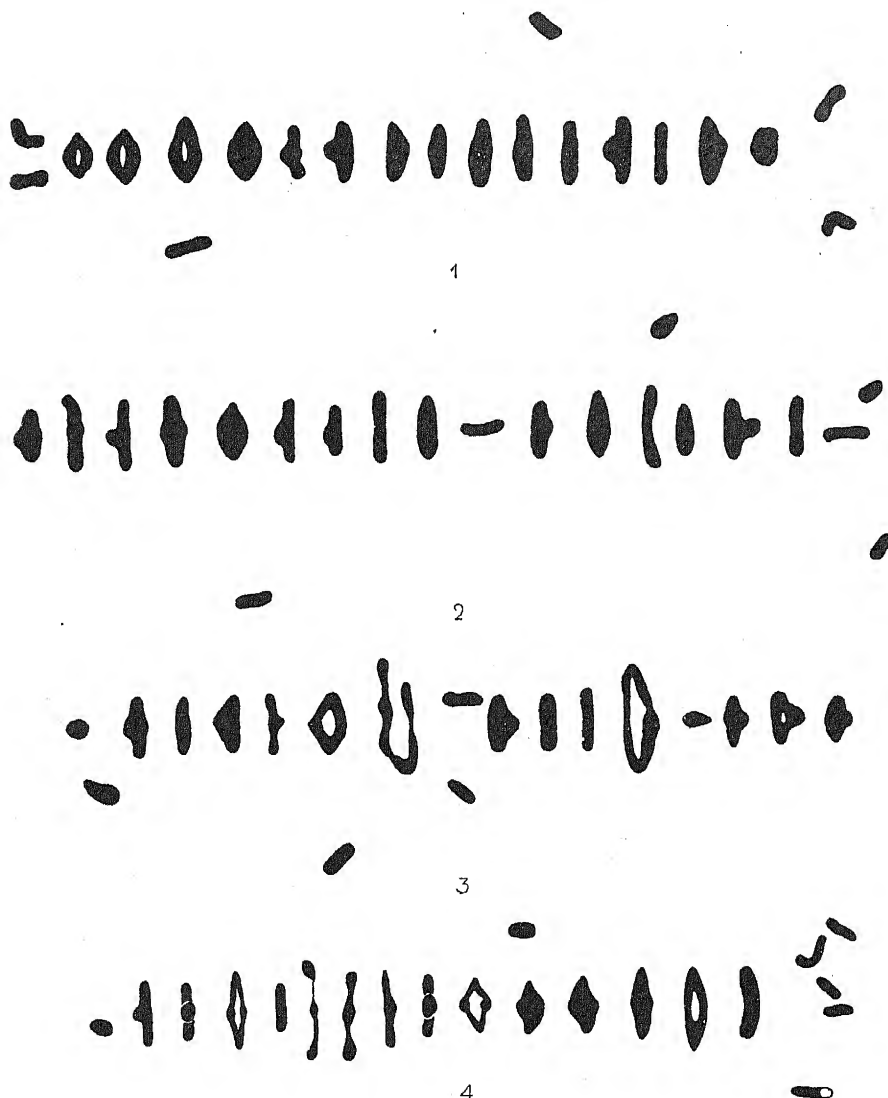
The variable number observed might be due, either to the presence of different numbers of univalents in different I—M groups or to the fact that the univalents in part lie at the same level as the metaphase group and are hidden by the bivalents. As a rule the latter possibility seems to be the correct one. In five cases in which it was possible to analyse complete I—M groups the number of univalents present was always six. Figs. 1—2 show two complete I—M groups in side view. In both cases the chromosome complement consists of  $15_{II} + 6_I$ . Some univalents are lying in or near the equatorial plane and are difficult to distinguish immediately in contrast to the univalents lying more or less removed from the main bulk of chromosomes. In first metaphases, polar view, the rodshaped univalents are seen to be situated in the periphery and are easy to distinguish from the bivalents in the centre (figs. 6—7). In this respect the *Phleum* hybrids behave in the same way as the pentaploid wheat hybrids (cf. KIHARA 1924, p. 22). In figs. 6 and 7 there are again  $15_{II} + 6_I$ .

Not infrequently, however, quadrivalents in the shape of rings or chains were observed at I—M (figs. 3 and 5). This does not necessarily influence the number of univalents. In fig. 3, I—M in side view, there are 2 quadrivalents, 11 bivalents and 6 univalents.

In both *nodosum* and *pratense* (figs. 26 and 29) the bivalents are as a rule ringshaped with two terminal chiasmata or rodshaped with one chiasma. They are of the same type as those studied by PERO (1933) and RANCKEN (1934) in species and hybrids of *Festuca* and *Lolium*. In *P. nodosum* the chiasma frequency in 33 complete metaphase groups was calculated and gave the average value of 1.82 chiasmata per bivalent. In *P. pratense* and the hybrids the chromosomes were too numerous and the fixations not sufficiently good to permit a comparative study of chiasma frequency. However, judging from figs. 1—4, chiasma frequency in the hybrids does not seem to be lower than in *nodosum*.

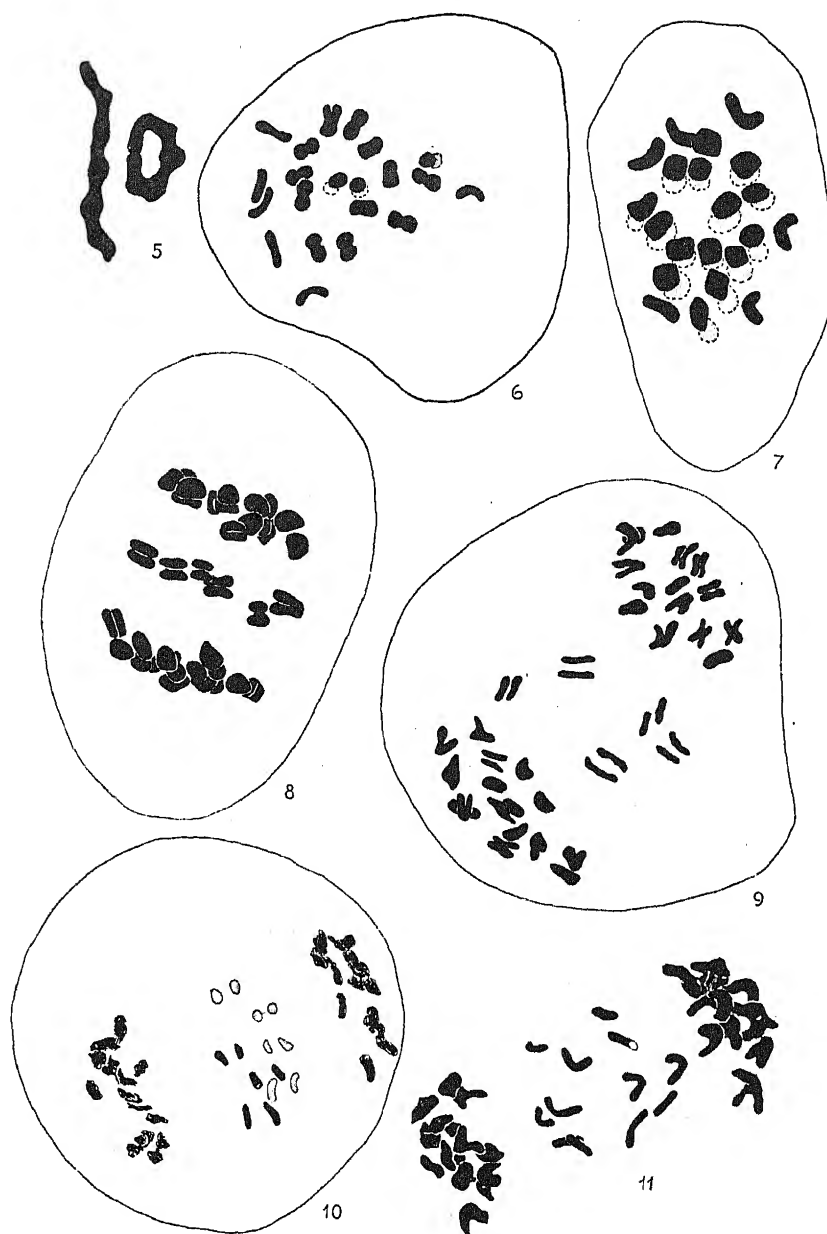
At first anaphase the bivalents and eventual quadrivalents separate, and then all or part of the univalents gather in the equatorial plane (fig. 8) and split (figs. 9—11) in the manner which is wellknown from the pentaploid wheat hybrids. In wheat all seven univalents always

divide at I—M (KIHARA 1924, p. 21) but in the *Phleum* hybrids the number of splitting univalents is variable. In the 36-chromosome plant

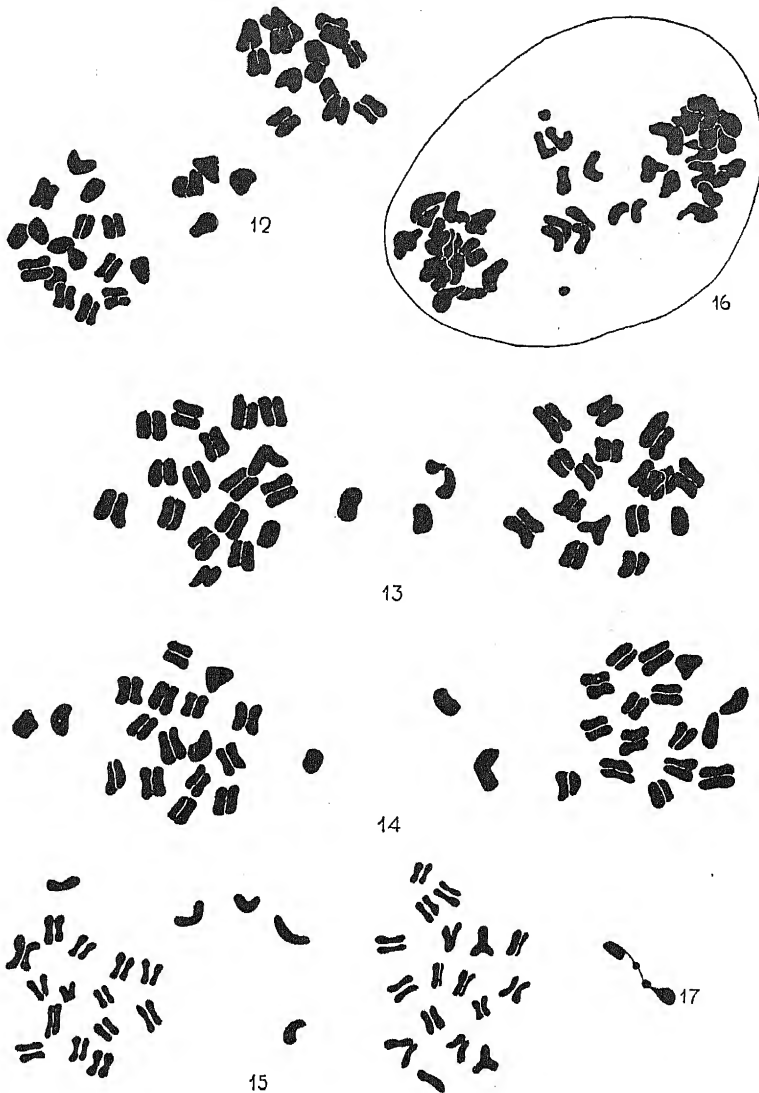


*Phleum pratense*  $\times$  *nodosum spont.* Meiosis in the pollen mother cells. Figs. 1—4, I—M-groups (separately drawn); figs. 1—3 from a hybrid with  $2n = 36$ , fig. 4 from a hybrid with 35 chromosomes; figs. 1—2,  $15_{II} + 6_I$ ; fig. 3,  $2_{IV} + 12_{II} + 6_I$ ; fig. 4,  $14_{II} + 7_I$ . —  $\times 3300$ .

under discussion division of 1—6 univalents was observed in the following frequency:



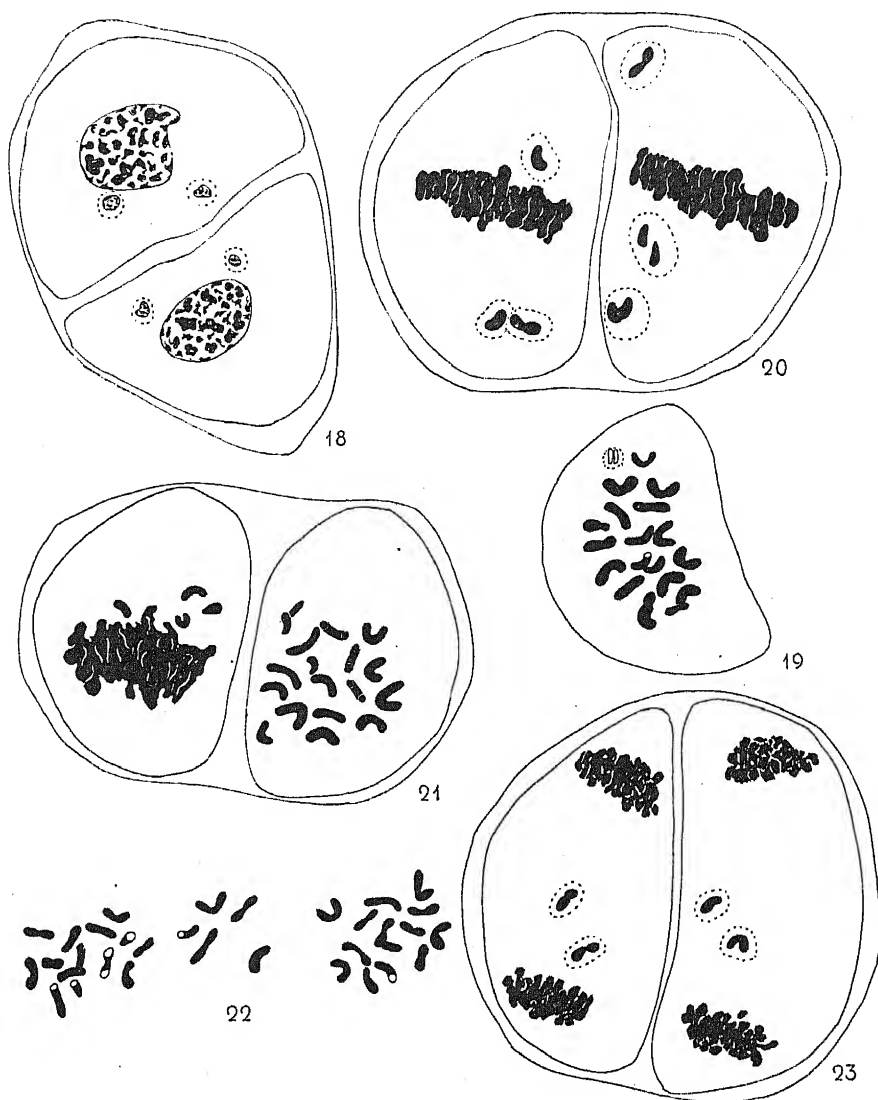
Figs. 5—11, meiosis in spontaneous *Phleum* hybrids (continued). Fig. 10 from a plant with  $2n = 35$ , the other pictures from a plant with 36 chromosomes. Fig. 5, two separate quadrivalents, figs. 6—7, I—M, polar view,  $15_{II} + 6I$ ; figs. 8—11, I—A; fig. 8, division of all six univalents, in each anaphase group 15 chromosomes; fig. 9, division of five univalents, distribution  $15-5-16$ ; fig. 10, division of seven univalents; fig. 11, late I—A, division of six univalents. —  $\times 3300$ .



Figs. 12—17, meiosis in spontaneous *Phleum* hybrids ( $2n=36$ ) (continued). Figs. 12—15, I—A showing the following distributions: fig. 12, 16—5—15; fig. 13, 17—3—16; fig. 14, 2—15—3—16; fig. 15, 15—4—17. Fig. 16, I—A, between the poles five dividing univalents and two fragments; fig. 17, a single I—M bivalent, separation of this bivalent will probably give rise to fragments. —  $\times 3300$ .

Number of univalents: ...	1	2	3	4	5	6	n	M $\pm$ m
Frequency: .....	2	15	24	41	13	5	100	3,63 $\pm$ 0,11

The variable number of dividing univalents might be caused either



Figs. 18—23, meiosis in spontaneous *Phleum* hybrids (continued). Figs. 18—23 are all from a hybrid with 35 chromosomes. Fig. 18, interphase, 4 micronuclei; fig. 20, II—M in side view, several chromosomes scattered in the plasma; fig. 19, II—M, polar view, one eliminated chromosome, 14 ordinary metachase chromosomes and 4 chromosomes which are probably half univalents; fig. 21, II—M, the plate in polar view seems to contain 14 ordinary chromosomes and 4 split univalents; fig. 22, II—A (separately drawn), 14 chromosomes in each anaphase group, 5 lagging chromosomes between the plates; fig. 23, II—A, side view, 2 lagging chromosomes in each cell. —  $\times 3300$ .

by the presence of different numbers of univalents at I—M or by the fact that some of them reach the poles undivided. The correctness of the latter alternative is evident, (a) from the observations mentioned



Figs. 24—25, II—A with lagging chromosomes in a spontaneous *Phleum* hybrid ( $2n = 35$ ); fig. 24, 4 laggards in each cell; fig. 25, 6 laggards in one cell, 7 in the other. Fig. 26, *Phleum nodosum*, I—M in side view (separately drawn),  $7n$ ; fig. 27, *Phleum alpinum* ( $4n$ ), I—M in polar view,  $14n$ ; figs. 28—29, *Phleum pratense*; fig. 28, I—A, distribution 21—21; fig. 29, I—M in side view (separately drawn),  $21n$  but indications of secondary association. —  $\times 3300$ .

above, concerning the number of univalents at I—M and (b) from observations on the chromosome distribution at I—A. In fig. 14 a first anaphase in polar view is represented. At different levels, from the

left to the right in the figure, the following chromosomes may be distinguished: a) two chromosomes of univalent type, that is without the split characteristic of anaphase chromosomes, which at I—M have been members of bivalents or multivalents, b) one of the anaphase plates, consisting of 15 chromosomes, c) 3 still undivided univalents between the anaphase plates, d) the other anaphase plate, containing 16 chromosomes. Also in this case there has probably been  $15_{II} + 6_I$  at I—M. Three of the univalents have been situated in or near the equatorial plane and are therefore now between the anaphase plates. Of the other three univalents, two have been lying near one of the poles and by their position they can be distinguished from the other anaphase group. The third univalent has been situated at the other pole and cannot now be distinguished from the other anaphase group, which has just arrived. — In fig. 15, showing another first anaphase, fixation and staining were favourable enough to elucidate rather accurately how the separation from I—M to I—A had proceeded. Between the anaphase plates there are four still undivided univalents. One of the plates (to the left in the figure) contains 14 typical and split anaphase chromosomes, and at the same level but in the periphery one unsplit chromosome of univalent type is visible. The other anaphase plate contains one chromosome of the same type in addition to 16 typical and split anaphase chromosomes. At I—M there has probably been one quadrivalent present, which is responsible for the distribution 14—16 instead of 15—15. Of the 6 univalents 4 have been at the equator, whereas the other 2 have been one at each pole and later joined the anaphase groups. — In a similar way the chromosome groups in figs. 12—13 may be interpreted. Here the distributions are 16—5—15 and 17—3—16 respectively. In the first anaphase represented by fig. 8 all six univalents lie at the equator, and in each anaphase group 15 chromosomes can be distinguished.

In a few cases fragments were observed at first anaphase. A typical case is represented by fig. 16 in which two fragments are present. In the *Phleum* hybrids such fragments were only found as exceptions, and therefore their origin could not be elucidated. However, the chromatin bridge at I—A represented by fig. 17 suggests that they are formed in a similar way to the fragments in a *Crepis* hybrid studied by the present writer (MÜNTZING 1934), viz. by crossing over in homologous segments with different position in the pairing chromosomes.

The divided univalents often lag and are not included in the interphase nuclei. Therefore micronuclei are almost regularly present at

interphase. Judging from their position each of the 4 micronuclei in fig. 18 has been formed by a half univalent. In 100 p. m. c. the number of micronuclei at interphase was determined with the following result:

Number of micronuclei: ..	0	1	2	3	4	5	6	7	8	n	$M \pm m$
Frequency: .....	8	12	30	13	22	8	4	2	1	100	$2,85 \pm 0,17$

Sometimes the micronuclei lie quite near the big interphase nuclei and have a chance to be included in the second metaphase plates. In other cases they are farther removed and retain this position at II—M (fig. 20). — The chromosomes in the II—M plates are rodshaped and did not fix well in the fixative used. Therefore only a few II—M plates could be accurately counted (figs. 19 and 21). In the best fixations and only with some difficulty on account of their smaller size could the former half univalents be distinguished from the other chromosomes. In figs. 19 and 21, which represent II—M plates in the hybrid with 35 chromosomes, there are probably 14 normal chromosomes and 4 half univalents. In fig. 19 there is in addition one eliminated chromosome at a different level.

Fig. 22 shows a second anaphase in polar view from the same 35-chromosome plant. There are 14 chromosomes in each plate and 5 chromosomes between the plates. As is to be expected from the division of univalents at I—A such lagging chromosomes (figs. 23—25) regularly occur at II—A. In the 36-chromosome hybrid their frequency was as follows:

Number of lagging chromosomes:	0	1	2	3	4	5	6	n	M ± m	
Frequency:	.....	3	7	22	30	27	9	2	100	3,06 ± 0,13

The average number is  $3,06 \pm 0,13$  and is consequently lower than  $3,63 \pm 0,11$ , the average number of univalents, dividing at I—A. This difference must be caused, partly by elimination of chromosomes at the first division, partly by the fact that some half univalents pass to the poles at the same time as the main bulk of chromosomes. This should occur in the second division just as well as in the first. — Several of the lagging chromosomes are not included in the telophase nuclei and form micronuclei. The number of micronuclei in 100 young tetrads was determined with the following result:

Number of														
micronuclei: 0	1	2	3	4	5	6	7	8	9	10	11	n	M ± m	
Frequency: .....	1	2	14	14	22	18	14	7	6	—	1	1	100	4,52 ± 0,20



As on an average  $4.52 \pm 0.20$  micronuclei are present in each tetrad and as every micronucleus has been formed by at least one chromosome, the average chromosome number of the male gametes must be lower than half of the somatic number 36. Indeed, the average value cannot be higher than 16—17.

In the 36-chromosome plant the typical I—M configuration was  $15_{II} + 6_I$  and six was the maximum number of univalents splitting at I—A. In the hybrid plant with 35 chromosomes the typical I—M configuration is evidently  $14_{II} + 7_I$ . This number of bivalents and univalents was present in the metaphase group represented by fig. 4, and at I—A as many as 7 univalents may divide (fig. 10). The number of univalents splitting at I—A in this plant was counted in one hundred cells. The following frequency was found:

Number of dividing univalents:	1	2	3	4	5	6	7	n	M $\pm$ m
Frequency:	.....	1	5	13	28	32	13	8	100 $4.56 \pm 0.13$

The average value is  $4.56 \pm 0.13$  and is significantly higher than  $3.63 \pm 0.11$ , the corresponding value of the plant with 36 chromosomes. The difference,  $0.93 \pm 0.17$ , proves that in the plant with 35 chromosomes there are more univalents at the first division than in the other plant, having  $2n = 36$ . This is also evident from the number of laggards at II—A. In the 35-chromosome plant this number was found to be  $3.77 \pm 0.13$ , the extreme values being 1 and 7. In the 36-chromosome hybrid the corresponding value was  $3.06 \pm 0.13$ . The difference is  $0.71 \pm 0.18$  and consequently significant. — Thus the direct observations that the 36-chromosome plant is characterized by  $15_{II} + 6$  at I—M and the 35-chromosome plant by  $14_{II} + 7_I$  is strongly supported by the number of univalents dividing at I—A and the number of chromosomes lagging at II—A.

The hybrids studied do not produce any unreduced pollen grains. Pollen from three of the hybrids and from two *nodosum* and two *pratense* biotypes was measured. The pollen was kept in a mixture of Bellings aceto-carmin fixative and glycerin. In the hybrids only morphologically good grains were measured. The size distribution was in all cases unimodal. The following average values and coefficients of variation (v) were obtained (Table 1). Each value is based on measurements of 150 grains and each unit in the table corresponds to  $1.11 \mu$ .

From the table it is evident that pollen size in the hybrids is on the average more variable than in the pure species. This is no doubt due to the fact that in the hybrids the pollen grains have different chromo-

TABLE 1. *Pollen grain size.*

Biotype	Somatic chromosome number	$M \pm m$	$v$
<i>nodosum</i> , No. .... 18	14	$28,78 \pm 0,21$	9,0
» » ..... 19	14	$27,82 \pm 0,24$	10,5
spont. hybrid, No. ... 23	36	$33,46 \pm 0,36$	13,3
» » » ... 24	36	$31,16 \pm 0,28$	10,8
» » » ... 26	35	$29,02 \pm 0,26$	11,0
<i>pratense</i> , ..... » ... 20	42	$33,26 \pm 0,14$	5,0
» ..... » ... 21	42	$33,08 \pm 0,17$	6,1

some numbers, and that in this case as in many other cases there is a positive correlation between chromosome number and pollen grain size. The *nodosum* biotypes measured have smaller pollen grains than *pratense*, the hybrids are on the average intermediate.

### III. THE $I_1$ -PROGENIES.

#### A. VIABILITY AND MORPHOLOGICAL VARIATION.

In the spring of 1932 the seeds obtained after isolation of the five hybrid plants were germinated. From a total of 602 seeds 391 seedlings were obtained, which corresponds to 65 per cent of plants. Seeds from pure *pratense* germinate much better and give a higher plant percentage. The five different seed portions germinated to about the same extent and the differences between the per cent values were not significant.

Several plants died already as tiny seedlings, others died at somewhat later stages. When the seedlings had grown enough to be transplanted into pots for fixation of root tips, considerable differences in vigour became evident. This observation was fully confirmed by studies of the mature plants. Indeed, in the  $I_1$ -families there was every transition between early dying seedlings and highly vigorous and viable plants. Figs. 33—39 give an idea of the variation in viability. In this respect the  $I_1$ -generation presented the same pictures as  $F_2$ -generations in crosses between widely separated species.

In the summer of 1933 the weight of the plants was determined. At that time the original number of plants had been somewhat reduced. In addition to the plants which died as seedlings several perished in the winter of 1932—33. By such losses the number of plants had been

TABLE 2. *Phleum pratense* × *nodosum* spont. Plant weight in  $I_1$ .

Progeny No.	Plant weight in grams															n	M	
	0	50	100	150	200	250	300	350	400	450	500	550	600	650	700			750
1 (02+03) .....		1	—	—	1	—	1	—	2	1	1	—	—	1	—	—	8	369
2 (04+05) .....		6	3	3		3	1	3	1	3	1	—	—	1	1	—	28	254
3 (07+08) .....						1	—	2	—	1	1	—	—	1	—	—	6	441
4 (010+012).....		82	46	30	21	15	12	11	8	2	5	—	—	1	1	1	235	133
5 (013+014).....					1	—	—	—	—	—	—	—	1				2	—

TABLE 3. *Phleum pratense* × *nodosum* spont. Pollen fertility in  $I_1$ .

Progeny No.	Completely pollen sterile	Per cent completely pollen sterile plants	Per cent good pollen in the partially fertile plants										n	M
			30	40	50	60	70	80	90	100				
1 (02+03) .....	1	7					1	2	7	4			14	85.0
2 (04+05) .....	10	34	1				3	1	9	4			19	78.7
3 (07+08) .....	2	22		1	—			1	3	3			7	87.9
4 (010+012).....	123	56		7	15	28	23	17	6				96	69.8
5 (013+014).....	1	25					1	—	2				3	88.3

diminished from 391 to 319, that is by 18 per cent. Forty other plants were not weighed as they had been used in green house cultures and were not comparable to the plants in the field. — As is evident from table 2 the weight of the remaining plants varied from about 0 to 750 grams. The average weight of progeny 4, 133 gr., seems to be lower than that of progenies 1 and 2 (369 and 254 gr. respectively) but the differences are not significant. On account of the striking skewness of distribution, which is characteristic at least of progeny 4, the standard error of the mean has not been calculated.

Unfortunately the mother plants of the five  $I_1$ -progenies were not available for weighing at the same time as their daughter plants. In 1934, however, their weight was determined. Four clone plants of hybrid no. 2 (the mother of  $I_1$ -progeny no. 2) had the average weight 248 gr., three clone plants of hybrid no. 3 (mother of the big  $I_1$ -progeny no. 4) had the corresponding value 443. In 1934 the average weight of the plants was much lower than in 1933. In this year the weight of one hundred  $I_1$ -plants, chosen at random, was on an average 210,50, in 1934 the weight of the same plants was only 132,75. — When comparing the two mother plants weighed in 1934 with their daughter plants weighed in 1933, the weight of the former should consequently be multiplied by  $210,50 : 132,75 = 1,59$ , which results in the values 394 and 704. The corresponding average values of the  $I_1$ -progenies were 254 and 133 respectively (table 2). This calculation is not very accurate but in combination with the photographs (figs. 32—39) it clearly shows that most of the daughter plants are less vigorous than their mothers. The effect of inbreeding on vigour is in this case very striking.

Besides in vigour the  $I_1$ -plant varied strongly in all other respects, such as mode of growth, height, quantity of leaves, leaf colour, leaf dimensions, number of tillers, strawstiffness, panicle dimensions, earliness and so forth. The photographs, figs. 33—39, give an idea of this strong variation.

Especially interesting is the fact that many plants on account of their prostrate mode of growth and their small leaf- and panicle-dimensions (compare e. g. figs. 31 and 37) are habitually very similar to *P. nodosum*. On the other hand many  $I_1$ -plants (as in fig. 33) looked like typical *P. pratense*. Consequently the plants could be divided into three categories, *pratense* types, *nodosum* types and intermediates. The frequencies in those groups were 29, 68 and 133 respectively. — As mentioned above the hybrid mother plants cannot morphologically be distinguished from typical *pratense*, but in spite of this many of the

daughter plants are very similar to *nodosum*. The segregation of such types is in excellent accordance with the necessary assumption that the plants with 35 and 36 chromosomes are descendants from spontaneous hybrids between *P. pratense* and *nodosum*.

#### B. FERTILITY.

The same strong variation as in respect of vigour and morphology also characterized fertility in the  $I_1$ -families. — In order to measure this variation pollen fertility was examined, and the number of seeds per cm. of the panicle after open pollination were counted. Many plants had defective anthers and did not produce any pollen at all, others had

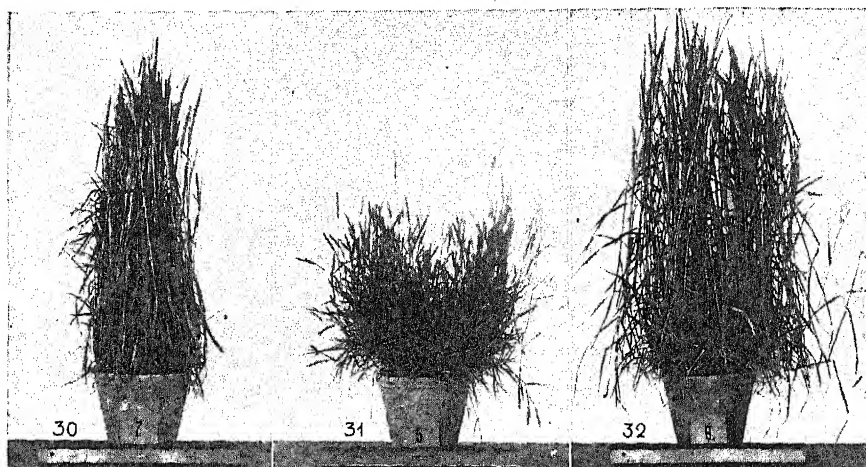


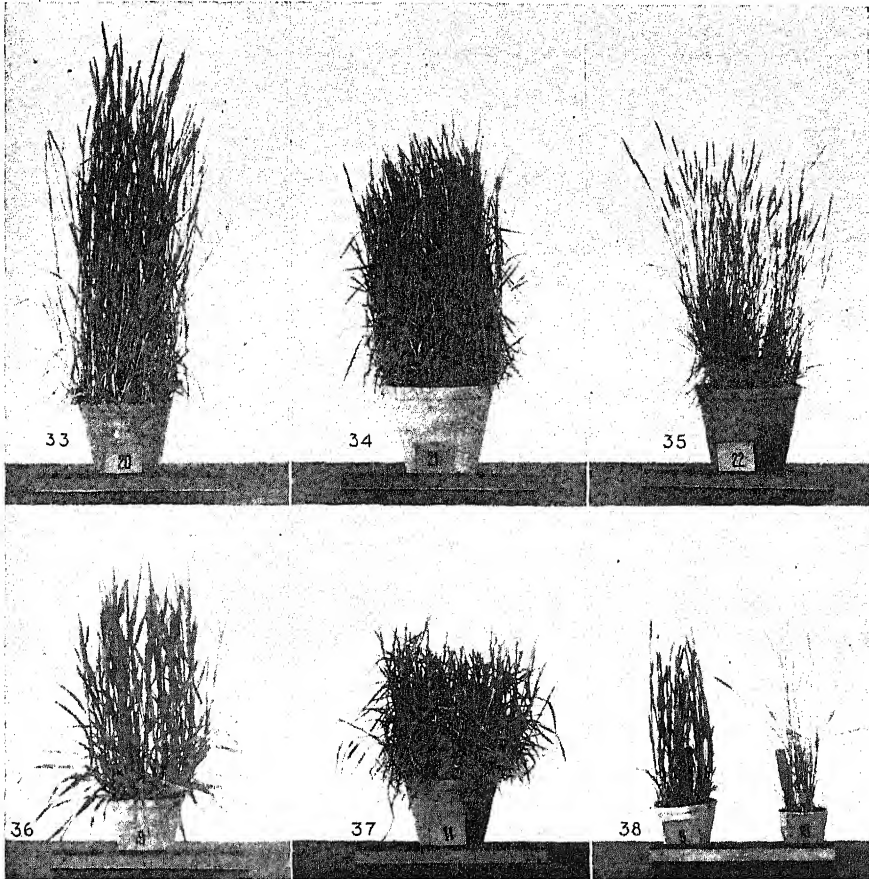
Fig. 30, *Phleum pratense* (the commercial variety »Gloria«); fig. 31, *Phleum nodosum*; fig. 32, a spontaneous hybrid with 36 chromosomes. (The length of the measure is 40 cm.).

pollen which as a rule was partially sterile. In such plants the percentage of morphologically good pollen grains was determined. The result is given in table 3.

Of the 276 plants examined not less than 137, that is 50 per cent, were completely male sterile. In the other plants the percentage of good pollen varied from 30 to 100. — The same strong variation and low average values were characteristic of the seed production after open pollination. As may be seen from table 4 the number of seeds per cm. of the panicle varied from 0 to 110.

As in the case of weight also pollen fertility and seed production are on the average lower in  $I_1$  than in the mother plants. The big progeny no. 4 (table 4) had an average seed production of 11,0 seeds

per cm. whereas the mother plant had the corresponding value 44. Concerning pollen fertility the mother plant had 85,4 per cent good pollen, but in the progeny not less than 56 per cent of the plants were completely male sterile. The partially fertile plants in the same progeny



Figs. 33—38, some different  $I_1$ -plants, obtained by selfing of the mother hybrid represented in fig. 32. The somatic chromosome numbers in these plants are the following: fig. 33,  $2n = 38$ ; fig. 34,  $2n = 37$ ; fig. 35,  $2n = \pm 34$ ; fig. 36 not yet determined; fig. 37,  $2n = \pm 38$ ; fig. 38,  $2n = 38$  (plant 9) and  $2n = \pm 33$  (plant 10). (The length of the measure is 40 cm.).

had the average value 69,8 per cent good pollen which is 15 per cent lower than the value of the mother plant. The same decrease in fertility is also met with in progeny 2 and is probably characteristic of the entire  $I_1$ -generation.

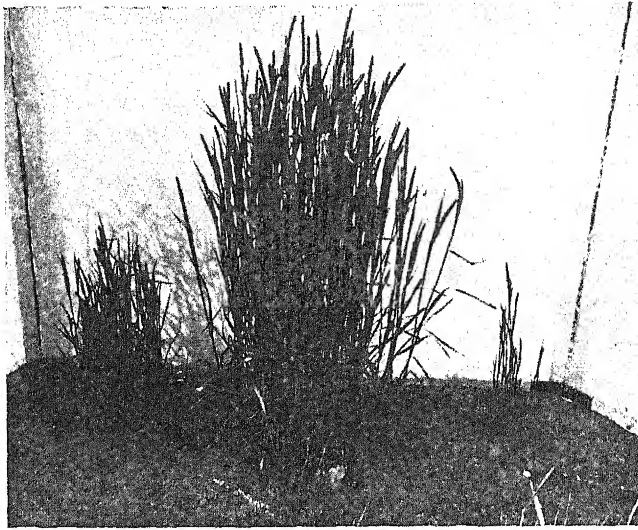


Fig. 39. Three  $I_1$ -plants (sister plants) growing in the field. The differences in vigour are striking.

### C. CHROMOSOME NUMBERS.

In order to determine the somatic chromosome numbers root tips of the young  $I_1$ -plants were fixed in diluted chromacetic formalin and stained with gentian violet. On the average this method was satisfactory. Some fixations were excellent and gave somatic plates which were easy to count, in other cases determination of the chromosome number proved to be difficult or impossible. Thanks to assistance by my co-workers Mr. R. LAMM and Miss M. PALM the chromosome numbers of 301  $I_1$ -plants have been determined. The result of those counts are given in table 5. Somatic plates with different chromosome numbers are represented by figs. 40—51.

The chromosome numbers in  $I_1$  vary between 29 and 43 and the average values of the five families range from  $36,4$  to  $39,4$ . Immediately striking is the fact that on the average the  $I_1$ -plants have higher chromosome numbers than their mother plants. The increase in the five progenies is  $+2,9$ ,  $+2,2$ ,  $+3,4$  (or  $4,4$ ),  $+0,4$  and  $+3,7$  respectively.

As shown by the meiotic studies the hybrids with 35 and 36 chromosomes were characterized by the chromosome formulae  $14_{II} + 7_I$  and  $15_{II} + 6_I$  respectively. Assuming random distribution of the uni-

TABLE 4. *Phleum pratense* × *nodosum* spont. Seed setting in  $I_1$ .

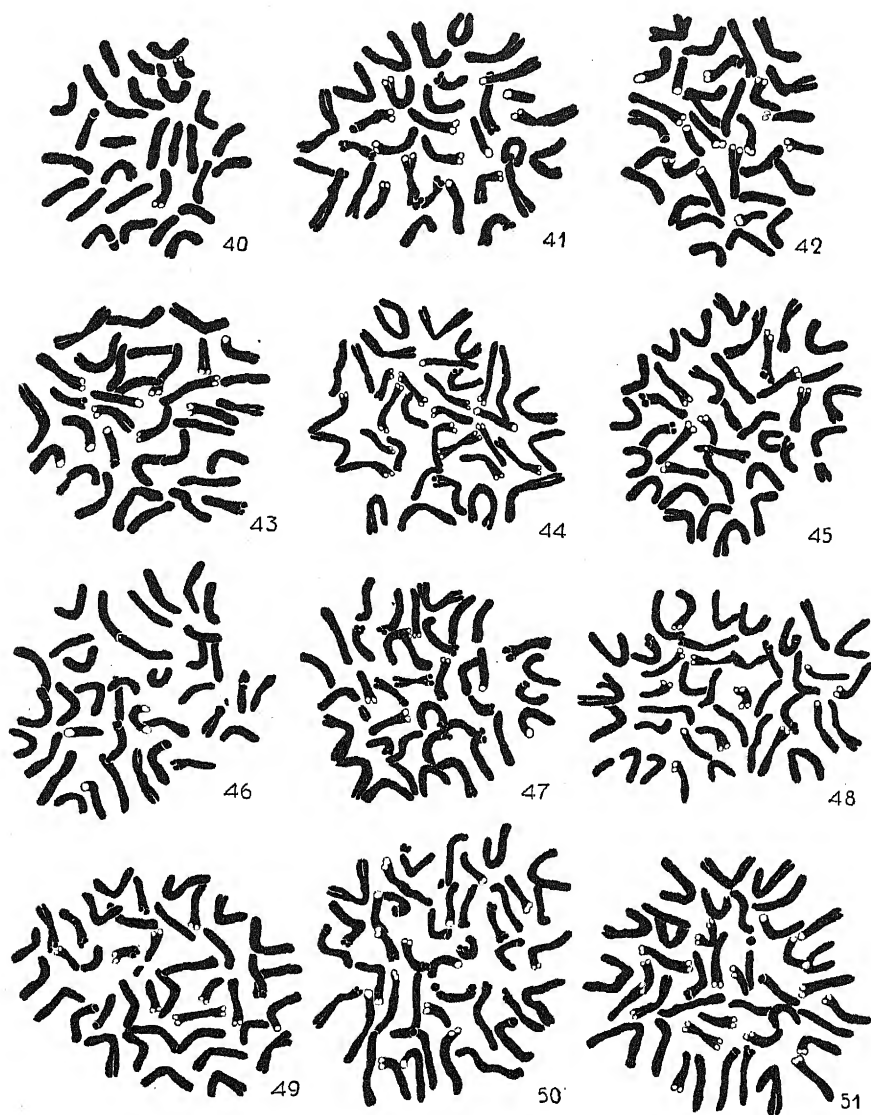
Progeny No.	Number of seeds per cm. of the panicle												n	M	Average seed production of the mother plant
	0	10	20	30	40	50	60	70	80	90	100	110			
1 (02 + 03) .....	1	—	2	—	2	1							6	33,3	—
2 (04 + 05) .....	16	4	1	1	1								23	10,7	23
3 (07 + 08) .....	2	—	—	—	3	1							6	33,3	—
4 (010 + 012) .....	154	37	15	5	2	3	1	3	—	—	1		221	11,0	44
5 (013 + 014) .....	1	—	—	1									2	—	31

TABLE 5. *Phleum pratense* × *nodosum* spont. Somatic chromosome numbers in  $I_1$ .

Progeny No.	Somatic chromosome numbers															n	M	Chromosome number of the mother plants
	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43			
1 (02+03) .....							1	1	1	3	3	1				10	37, <sup>9</sup>	35
2 (04+05) .....				1	—	—	3	3	5	6	7	4	3	3		35	38, <sup>3</sup>	36
3 (07+08) .....									1	1	2	1	1	2		7	39, <sup>4</sup>	35—36
4 (010+012).....	1	—	1	2	6	9	9	7	55	34	5	9	4	3	1	245	36, <sup>4</sup>	36
5 (013+014).....							1	1	—	—	—	—	—	2		4	38, <sup>5</sup>	35



valents, the average chromosome number of the progeny should be the same as that of the mother individual, and plants with high and low chromosome numbers should be formed with equal frequency.



Figs. 40—51, somatic chromosomes of different  $l_1$ -plants. Fig. 40,  $2n = 29$ ; fig. 41,  $2n = 32$ , fig. 42,  $2n = 33$ ; fig. 43  $2n = 34$ ; fig. 44,  $2n = 35$ ; fig. 45,  $2n = 36$ ; fig. 46,  $2n = 37$ ; fig. 47,  $2n = 38$ ; fig. 48,  $2n = 39$ ; fig. 49,  $2n = 40$ ; fig. 50,  $2n = 41$ ; fig. 51,  $2n = 42$ . —  $\times 2500$ .

But as elimination of chromosomes was observed to be frequent in the pollen mother cells, the average chromosome number of the progeny should in fact be somewhat lower than that of the mother plant. — As, on the contrary, the progenies showed a marked increase in chromosome number some counteracting processes must have been at work, e. g. selective gametic or zygotic viability or selective fertilisation.

In addition to the chromosome numbers given in table 5 a few more extreme values were obtained. One plant in family 4 had  $2n = 24$ , another plant  $\pm 71$  chromosomes. Both these plants died at an early stage and therefore it could not be controlled if they were true daughter plants or intermixtures of some kind. Another plant which is still alive had 18 chromosomes in some root tips, 36 chromosomes in others. Finally in family 5 one plant of *nodosum* type was found to be diploid ( $2n = 14$ ). This plant probably, but not necessarily (cf. NISHIYAMA 1933), represented an intermixture of *P. nodosum*.

With the exception of those aberrant individuals and a plant with  $\pm 43$  chromosomes, the highest chromosome number observed in the progenies is 42. This is to be expected from the chromosome formulae of the mother plants ( $15_{II} + 6_I$  and  $14_{II} + 7_I$ ). Formation of unreduced gametes was not observed in the mother plants and with the exception of the plant which possibly had  $\pm 71$  chromosomes polyploids did not appear in the progenies.

#### D. CORRELATIONS.

##### a) CORRELATIONS BETWEEN CHROMOSOME NUMBER AND VIGOUR.

In  $I_1$  both chromosome number and vigour varied very much. The presence of a marked positive correlation between these variables is at once evident from table 6. In the chromosome number class 33—35 (plants with 33 and 34 chromosomes) the average weight is 74 gr. and from this class the weight continuously increases to the chromosome class 41—43 in which the average weight is 405 gr. or more than five times as high. As the maximal chromosome number 42 is the same number as is characteristic of *P. pratense* the correlation may also be expressed in the following way: *in  $I_1$  plant vigour increases as the chromosome number approaches 42, the normal chromosome number of timothy*. The coefficient of correlation could not be calculated in this case as the X-series is extremely skew and the regression probably not straight-line. However, the data in table 6 are sufficient to demonstrate beyond doubt the presence of a marked positive correlation between chromosome number and vigour.

TABLE 6. *Phleum pratense* × *nodosum* spont. Correlation between chromosome number and weight.

2n:	Plant weight									n	M
	0	100	200	300	400	500	600	700	800 gr.		
31	1	1								2	—
33	16	5								21	74
35	46	15	10	3	—	—	2			76	135
37	41	20	15	7	4	1	—	1		89	161
39	7	6	6	9	8	2	2			40	298
41	1	1	—	3	3	1	2			11	405
43	112	48	31	22	15	4	6	1		239	—

## b) CORRELATION BETWEEN CHROMOSOME NUMBER AND HABITUS.

On account of the positive correlation between chromosome number and vigour a correlation between chromosome number and habitus seemed to be likely.  $I_1$ -plants of *pratense* type are as a rule more vigorous than  $I_1$ -plants of *nodosum* type and the former plants

TABLE 7. *Phleum pratense* × *nodosum* spont. Correlation between chromosome number and habitus.

Habitus	Somatic chromosome numbers							n	M ± m
	31	33	35	37	39	41	43		
<i>nodosum</i> types.....	1	9	30	27	7	1		75	$36,36 \pm 0,21$
intermediates .....	3	20	54	72	27	10		186	$37,40 \pm 0,15$
<i>pratense</i> types .....		2	4	8	10	7		31	$39,04 \pm 0,45$

might be expected to have a higher chromosome number than the latter. This was found to be true (table 7). The three  $I_1$ -groups, *nodosum* types, intermediates and *pratense* type had the following average chromosome numbers,  $36,36 \pm 0,21$ ,  $37,40 \pm 0,15$  and  $39,04 \pm 0,45$  respectively. The difference between the values of the *nodosum* and *pratense* types is  $2,78 \pm 0,50$  and consequently significant. Though this shows that the  $I_1$ -plants which are similar to *nodosum* have the lowest chromosome

numbers, these plants have on the average more than twice as many chromosomes as genuine, diploid *P. nodosum*.

c) CORRELATION BETWEEN CHROMOSOME NUMBER AND FERTILITY.

Not only vigour but also fertility increased parallel to the increase in chromosome number (table 8). Among the partially fertile plants the percentage of good pollen was 61,6 in the chromosome number class 35—37 and 85 in the class 41—43. Completely pollen sterile plants with shrivelled anthers or defective spikes were only found among the low chromosome number classes and the percentage of such

TABLE 8. *Correlation between chromosome number and pollen fertility.*

2n:	Completely sterile	Per cent completely sterile plants	Per cent good pollen in the partially fertile plants								n	M
			30	40	50	60	70	80	90	100		
31	1	—						1			1	
33	10	63			1	1	2	—	2		6	(66,7)
35	50	74	1	2	6	7	—	1	1		18	61,6
37	39	45		5	7	19	8	6	2		47	66,9
39	6	16					2	8	14	7	31	83,1
41	0	0						5	8	5	18	85,0
43	106	—	1	8	14	30	22	31	15		121	—

plants is inversely proportional to the chromosome number. In the class 35—37, 74 per cent of the plants were completely pollen sterile, in the class 39—41, 16 per cent and in the class 41—43, 0 per cent. Among the partially fertile plants the coefficient of correlation between chromosome number and percentage of good pollen was calculated and found to have the value  $+0,558$ . In FISHER (1930) table V. A. gives the significance of different values of the correlation coefficient for different n-values (up to 100). For  $n=100$  the odds that a correlation of  $+0,2540$  is significant are 99 to 1. As in our case the value of the correlation was much higher ( $+0,558$ ) and the number of individuals was 121, the significance of the correlation found is quite beyond doubt.

As described above seed production after open pollination was used as an approximate measure of female fertility. Positive correla-

tion was also found between seed production and chromosome number (table 9). As the chromosome number increases from 33 to 43 the average number of seeds per cm. of the panicle shows a continuous

TABLE 9. *Phleum pratense*  $\times$  *nodosum* spont. Correlation between chromosome numbers and seed setting (after open pollination).

2n :	Number of seeds per cm. of the panicle										n	M
	0	10	20	30	40	50	60	70	80			
31	1										1	—
33	16      1										17	5,6
35	59   11      1										71	6,8
37	46   19   13      3      1      1										83	12,6
39	14      7      1      3      6      2      —      1										34	22,4
41	3      2      —      1      2      1      1      2										12	36,7
43	139   40   15      7      9      4      1      3										218	—

increase from 5,<sub>6</sub> to 36,<sub>7</sub>. As the distribution of seed number is quite skew, the coefficient of correlation and the standard errors of the means have not been calculated, but nevertheless the significance of the correlation is evident.

#### d) CORRELATION BETWEEN POLLEN FERTILITY AND SEED PRODUCTION.

As might be expected male and female fertility are correlated (table 10). The completely male sterile plants had an average seed production (after open pollination) of 5,<sub>2</sub> seeds per cm. of the panicle, whereas completely pollen fertile plants with 90 to 100 per cent good pollen had the corresponding value 45,<sub>3</sub>. In the partially pollen sterile plants seed production was intermediate. Also in this case the coefficient of correlation has not been calculated on account of the skewness of the X-series.

#### e) CORRELATION BETWEEN VIGOUR AND RESULT OF FIXATION.

As mentioned above root tips of the young  $I_1$ -plants were fixed when the plants were growing in small pots. Part of those fixations

were quite good, others were more or less poor. This was observed to be the case even among plants which had been fixed on the same

TABLE 10. *Phleum pratense*  $\times$  *nodosum* spont. Correlation between pollen fertility and seed setting.

Per cent good pollen	Number of seeds pr cm. of the panicle												n	M
	0	10	20	30	40	50	60	70	80	90	100	110		
0	108	8	3	3	1								123	5.2
10	1												1	—
20														
30	1												1	—
40	4	1	1										6	14.5
50	5	3	3										11	14.8
60	12	10	4	1									27	14.8
70	8	9	2	2	2	—	—	1					24	15.2
80	7	7	3	1	4	4	—	1					27	25.2
90	1	1	1	2	2	1	1	2	—	—	1		12	45.3
100	39	31	14	6	8	5	1	4	—	—	1		109	—

occasion and which consequently had been in the same environment before and at the time of fixing. The observed differences in fixation

TABLE 11. Correlation between vegetative vigour and the result of fixation.

Result of fixation	Vigour				n	M
	1	2	3	4		
good.....	6	9	14	4	33	2.48
mediocre ...	30	33	28	1	92	2.00
poor.....	50	43	25	9	127	1.94

might therefore be caused by genotypical differences between the plants. — Upon closer examination it was found that the best fixations came from vigorous plants, the other fixations from weaker plants. At

the time of fixing this difference in vigour was not very obvious but became more striking later on, when the plants were fullgrown.

In the summer of 1932 when the plants had been transplanted to the field and started to flower their vigour was estimated. A scale from 1 to 4 was used, the most vigorous plants receiving the value 4 and vice versa. By studying the cytological drawings the fixations could be divided into 33 good, 92 mediocre and 127 poor fixations. The average vigour in these three groups was 2.48, 2.00 and 1.94 respectively (table 11). It should also be observed that the maximum class in the first group has the value 3, in the second group 2 and in the third 1. To get a mathematical value for this correlation the three distributions were tested by FISHER's  $\chi^2$ -method (FISHER 1930, p. 75). The  $\chi^2$ -value obtained was 16.37, and as there are 6 degrees of freedom this gives a probability value of 0.01. Thus the odds are 99 : 1 that the three series represent different distributions and that there is a positive correlation between plant vigour and result of fixation.

This correlation may be caused by the fact that already at an early stage the plants that afterwards become vigorous grow more rapidly and have a higher frequency of cell division in the root tips. On that account there are more chromosome plates available for selection and a better chance to find really good ones. This, however, is probably not the only or even the most important cause. In a poor fixation, in which the majority of the plates are bad, there are very seldom any good plates at all. Therefore, not only the speed of cell division but also the entire physiological condition of the plant and the root tips is probably of prime importance.

It may also be mentioned that fixations were made at different temperatures varying between 12° and 25° C. but no influence of temperature on the result of fixation could be detected.

#### IV. DISCUSSION.

There is a comprehensive literature on the systematical position, history of cultivation and breeding technique of timothy (cf. WITTE 1915, VALLE 1931). Cyto-genetic studies in the genus, however, have previously been undertaken only by GREGOR and SANSOME (1930). The material used by these authors was hexaploid and diploid *pratense* and tetraploid and diploid *alpinum*. On account of the breeding results and chromosome numbers GREGOR (1931) describes the diploid *pratense* as ecospecies *Phleum pratense diploidium*. Though it cannot be proved

that the *Phleum nodosum* described by LINNÉ was diploid, still it is rather probable. For this reason and for the sake of brevity the diploid type is in this paper referred to as *P. nodosum* L., the hexaploid as *P. pratense* L.

In the experiments of GREGOR and SANSOME crosses between *nodosum* and tetraploid *alpinum* easily gave hybrids. The combination *pratense* × tetraploid *alpinum* also succeeded though with some difficulty. Crosses between *nodosum* and *pratense*, however, failed completely and hybrids could not be obtained in spite of repeated efforts (GREGOR and SANSOME 1930, p. 376, GREGOR 1931, p. 207). In the present paper the plants studied have been assumed to be descendants of spontaneous crosses between *P. nodosum* and *pratense*. This assumption is consequently in conflict with the experimental results of GREGOR and SANSOME. However, the cytological results and the breeding behaviour of the plants described in the present paper clearly demonstrate that they are really descendants of hybrids between *pratense* and *nodosum*.

Only one other possibility needs to be considered, viz. that the chromosome number in *Phleum pratense* is not stable and that aberrants with higher and lower number may be formed in the same way as e. g. in *Dactylis glomerata* (MÜNTZING 1933). This possibility, however, must be rejected as *Phleum pratense* in contrast to *Dactylis glomerata* does not form any multivalents at meiosis (cf. fig. 29). Further, not a single plant of the 26 *pratense* types originally examined had a higher number than 42. If aberrants with higher or lower chromosome number than 42 occurred in *pratense*, plants with higher numbers should be equally frequent as plants with such low numbers as 35 or 36.

Consequently, hybrids between *pratense* and *nodosum* may really be formed and these species, which may rightly be called ecospecies (GREGOR 1931, p. 212), are not separated by an *absolute* barrier of incompatibility. It is natural, however, that hybrids have a greater chance to arise spontaneously in big experimental fields than in artificial crosses on a material, which must necessarily be much more limited.

The established correlations between chromosome number, vigour and fertility in the hybrids are important for the interpretation of their constitution. At first sight these correlations are impossible to explain. — In the progeny from pentaploid wheat hybrids chromosome number, vigour and fertility are correlated in quite a different way. As is well-known the work of KIHARA and others has demonstrated that the progeny from pentaploid wheat hybrids separates itself into one »Ver-



mehrungsgruppe» and one »Verminderungsgruppe». In consecutive generations the chromosome numbers in these groups are changed in a plus and minus direction respectively, and the final result is a reversion to 42 and 28, the chromosome numbers of the parent species. In the increase group (plants with 36—42 chromosomes) fertility increases parallel to the increase in chromosome number (KIHARA 1924, p. 111). In the decrease group, plants with 28—34 chromosomes, fertility increases as the chromosome number *decreases* (KIHARA l. c., MORIYA 1932). In this group the plants with the lowest number, 28, have the best fertility. In the *Phleum* material, on the contrary, there is a continuous decrease in fertility as the chromosome number gets lower. The plants with the lowest chromosome number have here the poorest fertility.

Another still more marked difference between the *Phleum* material and the pentaploid wheat hybrids is the fact that in the latter the plants with low chromosome numbers have normal vigour (WATKINS 1930, p. 208). In *Phleum* the plants with low chromosome numbers have on the average very poor viability. These bad *Phleum* plants are similar to the so-called »sterile» combinations which sometimes appear in the increase group of the pentaploid wheat hybrids. In most of the plants in the increase group the sum of bivalents and univalents is 21 but in a few exceptional plants this sum has other values than 21. Such plants lack one or more of the specific *vulgare* chromosomes, that is the chromosomes which appear as univalents at meiosis in hybrids between *Triticum vulgare* and representatives of the emmer-group. Those sterile combinations have low viability and fertility (cf. KIHARA 1924, WATKINS 1930). On the basis of those conditions in wheat and the work of GREGOR and SANSOME the following interpretation of the present results in *Phleum* is the most probable one.

After crosses between *nodosum* (2n) and *alpinum* (4n) GREGOR and SANSOME (1930) obtained triploid hybrids and in the progeny from those some hexaploid fertile plants. On account of this result the authors assume that *P. pratense* has arisen from crosses between *nodosum* and some other species »in a manner analogous to that described for the artificial hexaploid». In a later paper GREGOR (1931) reports that crosses between this artificial hexaploid and natural *pratense* easily succeeded and gave 161 hybrid plants, many of which were both male and female fertile. Thus there is good reason to believe that the genomes in *Phleum pratense* are at least partially homologous with the genomes in *P. nodosum* and *alpinum* (4n). In *P. alpinum* (4n) the two

genomes are evidently different as only bivalents and no quadrivalents are found at I—M (fig. 27).

The genomatic constitution of *nodosum*, *alpinum* ( $4n$ ) and *pratense* may therefore be written as  $NN$ ,  $AABB$  and  $NNAABB$  respectively. The  $F_1$  hybrids between *pratense* and *nodosum* will consequently have the constitution  $\frac{N}{NAB}$ .

In such a hybrid the two  $N$  genomes will probably form 7 bivalents at first metaphase, the  $A$  and  $B$  chromosomes 14 univalents. As mentioned above (p. 104) the primary hybrids must have been back-crossed to *pratense*. The gametes of  $F_1$  will have from 7 to 21 chromosomes of the constitution  $N + 0 - 14$  ( $A + B$ ). In extreme cases the gametes will be  $NAB$  or  $N$ . When such gametes meet pure *pratense* gametes,  $NAB$ , the result will be  $\frac{NAB}{NAB}$  and  $\frac{N}{NAB}$ , that is hexaploid *pratense* plants and new  $F_1$  plants with 28 chromosomes. Such extreme plants, however, are only formed in two cases out of  $2^{14}$ . As a rule the back cross plants will get intermediate numbers, viz.  $2n = \pm 35$ . — Those plants have probably obtained a few  $A$  chromosomes and a few  $B$  chromosomes from the primary hybrid. If the seven  $A$  chromosomes are indicated by  $a_1 a_2 a_3 \dots a_7$  and the  $B$  chromosomes by  $b_1 b_2 b_3 \dots b_7$  a back cross plant with 35 chromosomes may have for instance the constitution  $Na_1 a_2 a_3 b_1 b_2 b_3 b_4 + NAB$ . At meiosis such a plant should form  $14_{II} + 7_I$ . Of the bivalents seven are formed by the  $N$  chromosomes, the others by  $a_1 a_2 a_3$  and  $b_1 b_2 b_3 b_4$  together with the corresponding chromosomes from the  $A$  and  $B$  genomes of *pratense*. The seven univalents are represented by the remaining *pratense* chromosomes, viz.  $a_4 a_5 a_6 a_7 + b_5 b_6 b_7$ .

Some of the hybrids found had  $2n = 36$ . According to the theory back cross plants with 36 chromosomes have arisen from the union of  $NAB$  gametes with 21 chromosomes from *pratense* and gametes with 15 chromosomes from the primary hybrid *pratense*  $\times$  *nodosum*. These gametes contain the seven  $N$  chromosomes plus eight chromosomes from the  $A$  and  $B$  genomes. These eight chromosomes will form bivalents with the corresponding *pratense* chromosomes, and the remaining *pratense* chromosomes will be univalents. This leads to formation of  $15_{II} + 6_I$  at meiosis, which was found to be characteristic of the spontaneous hybrids with 36 chromosomes. The hybrid with 35 chromosomes had  $14_{II} + 7_I$ , which also fits in with the theory.

These plants with 35 and 36 chromosomes are probably not the

immediate products of back crosses between  $F_1$  and *pratense* but may be the result of repeated back crosses to *pratense*. However, such secondary back cross plants with lower chromosome numbers than 42, will in principle have the same constitution as the primary back cross plants. The secondary back cross plants with  $2n = 36$  may then e. g. have the following constitution:

$$\frac{Na_1 a_2 a_3 a_4 b_1 b_2 b_3 b_4}{Na_1 a_2 a_3 a_4 b_1 b_2 b_3 b_4} + a_5 a_6 a_7 b_5 b_6 b_7$$

The gametes of such plant will all contain  $Na_1 a_2 a_3 a_4 b_1 b_2 b_3 b_4$  and in addition 0—6 of the chromosomes  $a_5 a_6 a_7 b_5 b_6 b_7$ . If in extreme cases all six univalents are included in a gamete and two such gametes unite when the plant is selffertilized the result will be a pure *pratense* plant with 42 chromosomes. If on the other hand all six univalents are lacking and two such gametes unite the result would be a plant with 30 chromosomes and having the following constitution:

$$\frac{Na_1 a_2 a_3 a_4 b_1 b_2 b_3 b_4}{Na_1 a_2 a_3 a_4 b_1 b_2 b_3 b_4}$$

*This plant only contains fractions of the A- and B-genomes. —* Deviations from entire multiples of a basic number are almost always accompanied by reduced viability and fertility. Therefore, *incompleteness of the A and B genomes is probably responsible for the low viability and fertility of those  $I_1$ -plants which have low chromosome numbers.* On account of the back crosses to *pratense* the hybrid mother plants with 35 and 36 chromosomes have probably complete A and B genomes and consequently good viability. When selffertilized, however, they must give rise to a multitude of plants with incomplete A and B genomes, which on this account are more or less unviable.

Returning to the chromosome formulae most of the gametes formed by the 36-chromosome plant will contain half of the six univalents,  $a_5 a_6 a_7 b_5 b_6 b_7$ , that is any three of these chromosomes. If two such gametes are united the following cases are possible: 1) The three univalents in one gamete (e. g.  $a_5 a_6 a_7$ ) are all different from the three univalents in the other one ( $b_5 b_6 b_7$ ). In this case the gametes complete each other and the resulting plant will have the same constitution as the mother plant and contain one complete A and one complete B genome. 2) The gametes may contain the univalents  $a_5 a_6 b_5$  and  $b_6 b_7 b_7$  respectively. The resulting plant will have an incomplete A genome (the  $a_7$  chromosome is lacking) and should form  $16_{II} + 4_I$  at meiosis.

3) Both gametes contain the same three univalents, e. g.  $a_5a_6b_6$ . In the resulting plant both the *A* and *B* genomes are incomplete (the  $a_7$ ,  $b_5$  and  $b_7$  chromosomes are lacking), and at meiosis 18 bivalents and no univalents should be formed.

In the plants with incomplete genomes the sum of bivalents and univalents will be lower than 21 and such plants correspond to the »sterile» combinations in the progeny of the pentaploid wheat hybrids. — Without giving further detailed instances it will easily be realized that the higher the chromosome numbers of gametes and zygotes, the greater is the chance of the *A* and *B* genomes being complete. As further in the  $I_1$ -plants a highly incomplete genome probably causes a lower viability and fertility than the absence of only one or two chromosomes, the result will be a positive correlation between chromosome number, viability and fertility.

In this connection it may be remembered that the  $I_1$ -plants with low chromosome numbers were often similar to *P. nodosum*. This may be due to the fact that such plants contain two complete *N* genomes and only fractions of the *A* and *B* genomes.

Sterility in the material studied is probably of two different kinds, diplontic and haplontic (cf. MÜNTZING 1930, p. 315). Diplontic sterility is due to the unfavourable genotypic constitution of the plant itself. Very often this kind of sterility is manifested by defective reproductive organs. On the other hand in cases of haplontic sterility the gametes, or more correctly the gones, die on account of their own lethal constitution. In the *Phleum* progenies many plants with low chromosome numbers showed diplontic sterility, that is they were completely »pollen sterile», having defective spikes or shrivelled anthers. In the plants with partially fertile pollen there was positive correlation between chromosome number and percentage of good pollen. In such plants at least part of the pollen sterility is probably haplontic. The gones formed by plants with high chromosome numbers will be more viable, as on the average they will contain more complete genomes than the gones of plants with lower chromosome numbers.

The explanation given above of the correlations observed has been advanced without considering the occasional occurrence of quadrivalents at meiosis. In spite of this the main traits of the theory should be correct. The quadrivalents probably arise on account of partial homology between different genomes, e. g. some *A* chromosomes may pair with *B* or *N* chromosomes. In the  $F_1$  hybrid *Phleum pratense* ( $6n$ )  $\times$  *P. alpinum* ( $4n$ ) GREGOR and SANSOME (1930) observed bivalents and

univalents but also »compound structures of higher valency». — In the pure species, *pratense*, *alpinum* ( $4n$ ) and *nodosum*, the present writer did not observe any quadrivalents at meiosis (figs. 26—29). In *P. pratense* there were indications of secondary association (fig. 29) but this needs further investigation.

In the  $I_1$ -families vigour and plant weight were on an average very poor, but as already emphasized there were all transitions between very weak and very robust individuals. The latter may be of interest from a practical point of view. A number of such vigorous plants, which have 42 or approximately 42 chromosomes and good fertility, have been selfed or crossed with each other. Progenies have been raised and are now grown in a comparative trial, using some well-known commercial varieties of timothy as testers.

It does not seem to be possible to extract types with higher chromosome numbers than 42 from the hybrid *Phleum* material. Neither the mother plants of the  $I_1$ -families nor their descendants have shown any marked tendency to form unreduced gametes. Only quite occasional giant pollen grains have been observed. Consequently, the final result in later generations will be a reversion to the hexaploid number 42 just as in the increase group of the pentaploid wheat hybrids. However, by recombination in the  $N$  genomes new products may be obtained which combine valuable characters from both parent species, *Phleum pratense* and *Phleum nodosum*.

### SUMMARY.

1) The chromosome numbers of a series of *Phleum* types, grown in the cultures of the Forage Crop Department of Svalöf, were determined. Besides a majority of hexaploid *pratense* and diploid *nodosum* plants some individuals were found to have  $2n = 35$  or 36. The ancestry and progeny of those plants demonstrate that they are descendants of spontaneous hybrids between *Phleum pratense* and *Phleum nodosum*.

2) The plants with  $2n = 35$  and 36 are characterized by the I—M configurations  $14_{II} + 7_I$  and  $15_{II} + 6_I$  respectively, but also quadrivalents may be observed. Part of the univalents split at I—A and lag at II—A. Micronuclei were frequent both at interphase and in the tetrads.

3) The  $I_1$ -families obtained by selfing mother plants with 35 and 36 chromosomes show a striking variation in morphology, vigour,

fertility and chromosome number. In those respects the  $I_1$ -families were similar to  $F_2$ -generations in crosses between widely different species.

4) Among the  $I_1$ -plants several positive correlations were established. Of most interest are the correlations between chromosome number and vigour and between chromosome number and fertility. As the chromosome numbers approach 42, the normal number of timothy, there is a marked increase in vigour and fertility.

5) The *nodosum* genome may be indicated by *N*, the *pratense* genomes by *NAB*. The absence of viable and fertile  $I_1$ -plants with low chromosome numbers is due to the fact that in such plants the *A* and *B* genomes are incomplete. As the chromosome number increases these genomes will be more and more complete and this results in plants with better vigour and fertility.

Svalöf, Cyto-Genetic Department of the Swedish Seed Association, October 1934.

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# TRIPLE HYBRIDS BETWEEN RYE AND TWO WHEAT SPECIES

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## I. INTRODUCTION.

**S**PONTANEOUS or artificial hybrids between wheat and rye have been well known for many years and have been described in numerous papers (cf. the summarizing papers of BLEIER 1928 and SCHIEMANN 1932). In most cases the wheat species used is *Triticum vulgare*, in a minority of cases representatives of the emmer group have been crossed to rye. BLEIER 1928, p. 368, cites a few such cases. More recently LONGLEY and SANDO (1930) have produced hybrids between *Triticum dicoccoides* and *Secale montanum* and in the same year PLOTNIKOWA (1930) describes hybrids obtained from the crosses *T. persicum* × rye and *T. durum* × rye. OEHLER (1931) and VASILJEV (1932) have also produced *durum* × rye hybrids. — All these hybrids between rye and wheat species belonging to the emmer group have hitherto been completely sterile, and no progeny has been obtained, not even in back crosses to the parent species.

In 1932 the present writer made a series of wheat × rye crosses, chiefly between *vulgare* and rye, but also using some different *turgidum* lines as female parents. In all, 1875 *turgidum* flowers were pollinated with rye pollen. After this cross pollination a fairly large number of seeds were obtained, but most of the kernels had very bad quality and were shrivelled or quite empty. A total of 280 seeds were considered as possibly viable and were placed for germination in sand moistened with Knop's solution. However, from those seeds only 7 plants were obtained. Thus, in this case only 0.37 per cent of the pollinated flowers gave viable hybrid plants.

From those plants root tips were fixed in the autumn and the somatic chromosome numbers determined. All the plants had the expected number 21 (7 rye + 14 *turgidum* chromosomes) and were therefore true hybrids. The plants wintered quite well, and in next spring and summer they developed into mature and very vigorous plants. In the early spring they were divided vegetatively according to OEHLER's method (OEHLER 1931, p. 359) and in this way 26 plants



were obtained from the original 7. Not only by their chromosome number but also by their morphological characters (cf. below), their vigour and their high degree of sterility did these plants prove to be true hybrids between *Triticum turgidum* and *Secale cereale*.

As is usual in wheat  $\times$  rye crosses the hybrids were completely male sterile, and self-fertilization was therefore excluded. Back crosses to the parent species would seem to be the best method to get progeny, but instead the hybrids were crossed to *T. vulgare*. This was tried on account of the following reasons:

In *Triticum* and in Angiosperms in general the union of gametes with different chromosome numbers often leads to poor embryos and poor seeds. This is probably due to disturbed chromosomal relations between the different tissues in the growing seed, embryo, endosperm and surrounding maternal tissues (cf. MÜNTZING 1930, 1933). — The hybrids in question were highly sterile, which was not unexpected, since no progeny had ever been obtained from hybrids between rye and representatives of the emmer group. Therefore it was assumed that if functional ovules were produced, they would probably be unreduced and contain 21 chromosomes. Under such circumstances back crosses to the parent species ( $n=7$  and 14 resp.) would mean union between gametes with different chromosome numbers and consequently lead to poor zygotes. On the other hand male gametes from *T. vulgare* ( $n=21$ ) should give good embryos with unreduced female gametes from the hybrid because these ovules should have the same chromosome number, 21, as the fertilizing pollen.

Consequently, instead of back crossing to the parents the cross (*turgidum*  $\times$  rye)  $\times$  *vulgare* was made as extensively as possible. A total of 3967 hybrid flowers were pollinated with *vulgare* pollen. This was done without previous castration as the hybrids were found to be completely male sterile. Much to our surprise seven rather well developed kernels were obtained from those crosses. — In the autumn of 1933 those kernels were germinated, and the result was 5 plants. These plants wintered well and in the following summer they grew into mature, well developed individuals. At the seedling stage root tips were fixed and the chromosome numbers determined with the following result: Three of the five plants had exactly 42 chromosomes (fig. 4), one plant had  $2n=41$  and one plant  $2n=\pm 40$ .

From this result the following conclusions can be drawn: a) the *turgidum*  $\times$  *Secale* hybrids form functional, female gametes with the somatic or approximately somatic chromosome number, b) those

gametes + *vulgare* gametes with the same chromosome number may give well developed seeds, which are capable of germination and further development.

## II. MORPHOLOGY OF THE HYBRIDS.

The morphological differences between rye, *Triticum turgidum* and *T. vulgare* are rather profound and numerous. As regards the present problem there is no reason to go too much into morphological details, only a few of the most striking differences will be discussed in the following pages. — On the average the hybrids were intermediate between the parents or showed a mixture of their characters.

TABLE 1. Measurements of ears and spikelets.

Species and hybrids	Ear length (in cm.)	Number of spikelets per ear	Ear density (spikelet number: ear length)	Number of flowers in the spikelets	Number of plants measured
<i>Secale cereale</i> .....	9,3	31,6	3,3	2,0	30
<i>T. turgidum</i> × <i>Secale</i> , $F_1$	16,0	31,5	2,0	6,5	11
<i>T. turgidum</i> .....	8,1	20,4	2,5	4,7	6
<i>T. vulgare</i> , »Drottivete»...	8,8	18,6	2,1	6,6	9
» , »Solvete III»	8,4	17,5	2,3	6,4	6
» , »Kronvete»...	9,8	17,1	1,8	6,9	5
<i>Triple hybrids</i> .....	12,1	25,8	2,2	5,7	10

A few morphological differences have been subjected to measurements. The average values of ear length, number of spikelets and number of flowers in each spikelet are given in table 1. The standard errors of the means have not been calculated as the number of individuals available was rather low. Anyhow, the values reflect some of the most striking morphological differences, which may also be seen in figs. 1—3.

### A. THE TURGIDUM × RYE HYBRIDS.

In rye there are only two flowers in each spikelet, in *T. turgidum* the number of flowers is variable but always higher than two. The average number was found to be 4,7 (table 1). In  $F_1$  there was dominance for *turgidum*, the number of flowers per spikelet (6,5) even being higher than in that species. Concerning the number of spikelets

per ear, however, rye was dominant, the numbers for rye, *turgidum* and  $F_1$  being 31,6, 20,4 and 31,5 respectively. The great number of big spikelets in  $F_1$  were carried by very long ears, which were much



Fig. 1. Ears of the triple hybrid and its parents. Upper row from the left to the right: *Secale cereale*, *Triticum turgidum*  $\times$  *Secale*,  $F_1$ , and *Triticum turgidum*; below, *Triticum vulgare* (left) and the triple hybrid, *Secale* + *T. turgidum* + *T. vulgare*, (right). The length of the measure is 20 cm.

longer than in both parent species. The average values of ear length were 16,0 ( $F_1$ ), 8,1 (*turgidum*) and 9,3 (rye). In  $F_1$  the long ear length is responsible for the fact that the number of spikelets per cm. of the ear was relatively low. This number was found to be 2,0 in  $F_1$ , whereas the corresponding values in *turgidum* and rye were higher (2,5 and 3,3).

The morphology of the glumes may be seen in figs. 2 and 3. In rye the empty glume is very small and narrow, in *turgidum* much bigger and broader. In  $F_1$  the empty glume is more like *turgidum* than rye, but the rye influence is quite marked. The apical tooth of *turgidum* is in  $F_1$  replaced by a short awn. — With respect to the flowering glume the differences between *turgidum* and rye are again very great.  $F_1$  is evidently intermediate (fig. 3).

TABLE 2. Height of *turgidum* × rye and *vulgare* × rye hybrids.

H y b r i d s	P l a n t h e i g h t i n c m.										n	M
	30	50	70	90	110	130	150	170	190			
<i>turgidum</i> × rye, exper. garden .....					4	3	3	3		13	123,8	
<i>vulgare</i> × rye, exper. garden .....		4	5	14	26	3				52	87,4	
<i>turgidum</i> × rye, green- house .....						2	6	2	2	12	146,6	
<i>vulgare</i> × rye, green- house .....			1	3	16	13	2			35	106,8	

As already mentioned the *turgidum* × rye hybrids were very vigorous and much taller than specimens of *turgidum*, growing near the  $F_1$  hybrids. But as no rye was cultivated under the same environmental conditions and only a few *turgidum* plants were available, the vigour of  $F_1$  in relation to the parent species could not be measured. However, the *turgidum* × rye plants were much more vigorous than a number of *vulgare* × rye hybrids growing under the same conditions. Hybrids of both kinds were grown partly in the experiment garden partly in the green-house. Those plants had the following heights (table 2).

The 14 *turgidum* plants had been obtained by vegetative division of seven original plants. Those hybrids represented different combinations between four *turgidum* and three rye varieties. As the differences between these varieties were rather slight no differences in

morphology or vigour between  $F_1$  plants from different combinations could be observed.

The *vulgare*  $\times$  rye hybrids also represented different combinations. The 87 plants measured had been obtained by vegetative propagation from 29 original hybrids and those hybrids were the products of crosses involving 11 different *vulgare* biotypes and 3 rye varieties.

As is evident from table 2 there is a quite clear difference between the vigour of the two kinds of hybrids. In the experiment garden the *turgidum*  $\times$  rye plants were on the average 41 per cent taller than the *vulgare*  $\times$  rye hybrids and in the green-house the corresponding value was 37 per cent.

#### B. THE TRIPLE HYBRIDS.

The triple hybrids, obtained from the cross (*turgidum*  $\times$  rye)  $\times$  *vulgare*, were habitually rather *vulgare* like (fig. 1) but upon closer examination the influence of all three parent species could be clearly observed. This is evident from the photographs of spikelets (fig. 2) and glumes (fig. 3). The most striking influence of the *vulgare* genomes is the removal of the long awns, present on the flowering glumes of both rye, *turgidum* and *turgidum*  $\times$  rye,  $F_1$ . The *vulgare* varieties used for the crosses («Kronvete», «Drottvet» and «Solvete III») were all awnless and as in crosses between *vulgare* varieties with and without awns the absence of awns is almost completely dominant (figs. 1—3).

The glumes of the triple hybrids were on the average intermediate between those of *turgidum*  $\times$  rye,  $F_1$ , and *vulgare* (fig. 3). In *vulgare* the empty glumes are broad, without keel but with an apical tooth and, in the varieties used, glabrous. In the triple hybrids the sharp keel present in *turgidum* and rye was dominant and also the hairiness of *turgidum*. The flowering glumes were rather similar to the empty glumes.

The triple hybrids had long ears (fig. 1) but not as long as those of the mother hybrid. According to table 1 the average values were 16,0 cm. for *turgidum*  $\times$  rye,  $F_1$  and 12,1 for the triple hybrids. *T. vulgare* has much shorter ears, the average values of three different biotypes being 8,8, 8,4 and 9,8 cm. Consequently, ear length in the triple hybrids is intermediate between the parents, *turgidum*  $\times$  rye,  $F_1$ , and *vulgare*. This is true also of the number of spikelets, which was found to be 31,5 in *turgidum*  $\times$  rye,  $F_1$ , 25,8 in the triple hybrids and 18,6, 17,5 and 17,1 in different *vulgare* biotypes. The average number of

flowers per spikelet, 5,7, is about the same or a little lower than in *turgidum*  $\times$  rye,  $F_1$ , and the different *vulgare* biotypes (table 1).

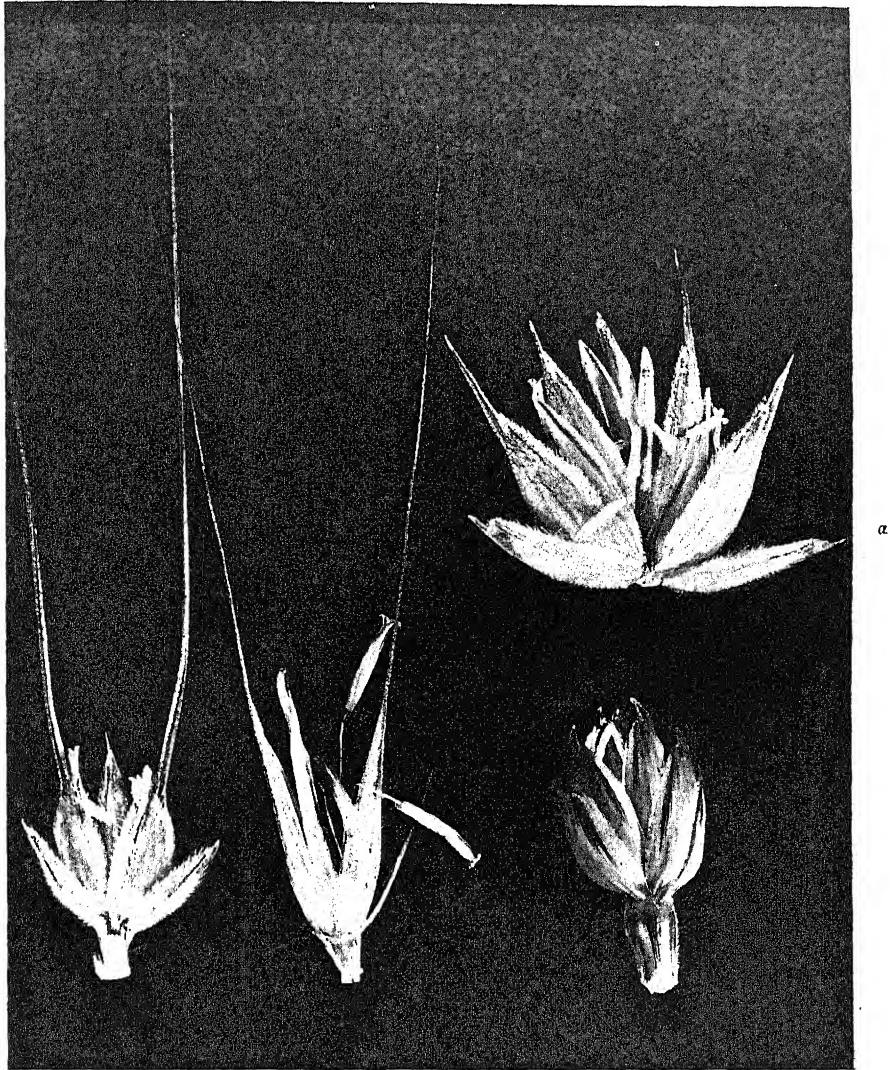


Fig. 2. Spikelets of the triple hybrid (a) and the parent species, *Triticum turgidum* (b), *Secale cereale* (c) and *Triticum vulgare* (d). —  $\times 2,0$ .

The triple hybrids were vigorous plants but not so tall as the mother plants, *turgidum*  $\times$  rye,  $F_1$ . They had about the same vigour

as *vulgare*  $\times$  rye,  $F_1$ , and were definitely more vigorous than pure *turgidum* and *vulgare*.

In the green-house the average height of 33 *vulgare* and 12 *turgidum* plants was 92,<sub>80</sub> and 109,<sub>20</sub> cm. respectively. The corresponding value of 29 *vulgare*  $\times$  rye,  $F_1$  plants was 119,<sub>74</sub> and of 5 triple hybrids

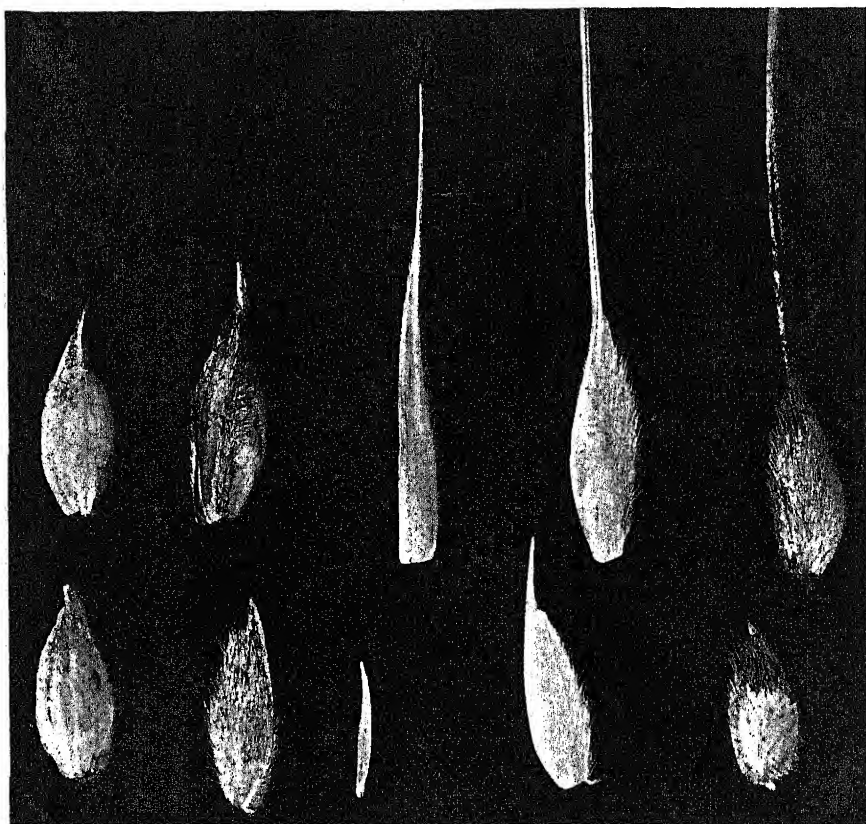


Fig. 3. Glumes of the triple hybrid and its parents. Upper row, flowering glumes, lower row, empty glumes. From the right to the left, *Triticum turgidum*, *T. turgidum*  $\times$  *Secale cereale*,  $F_1$ , *Secale cereale*, the triple hybrid (*turgidum*  $\times$  *Secale*  $\times$  *vulgare*) and *T. vulgare*. —  $\times 2.5$ .

120,<sub>0</sub>. In the experiment garden the relative height ran in the same order. The *vulgare* plants were lowest, 82,<sub>37</sub> cm. ( $n=94$ ) followed by *turgidum*, 103,<sub>30</sub> ( $n=22$ ) and *vulgare*  $\times$  rye,  $F_1$ , 104,<sub>81</sub> ( $n=39$ ). In the experiment garden only three triple hybrids were measured but these had the average value of 116,<sub>0</sub> cm. — *Turgidum*  $\times$  rye,  $F_1$  hybrids were not available in 1934, but as in 1933 those hybrids had been about

40 per cent taller than the *vulgare*  $\times$  rye plants it is evident that also in vigour the triple hybrids were intermediate between the parents, *turgidum*  $\times$  rye,  $F_1$  and *vulgare*.

The five different triple hybrids represented the following combinations of varieties: Two plants were obtained from (*turgidum*, »Rivets bearded»  $\times$  rye »0306»)  $\times$  *vulgare*, »Kronvete», one plant resulted from (»Rivets bearded»  $\times$  »0306»)  $\times$  *vulgare*, »Solvete III», one plant from (»Rivets bearded»  $\times$  »0306»)  $\times$  *vulgare*, »Drottvet», and the fifth plant, finally, from (*turgidum* var. *dinurum*  $\times$  »Sangasterye»)  $\times$  *vulgare*, »Kronvete». Thus, although several different varieties of *vulgare*, *turgidum* and rye were used for the crosses, the intraspecific differences were too small as compared with the interspecific ones to be distinguishable in the hybrids.

As mentioned above there were also differences in chromosome number, three of the five triple hybrids having  $2n=42$ , one individual  $2n=41$  and one  $2n=\pm 40$ . These chromosomal differences had no noticeable effect on morphology or vigour but a very marked influence on fertility.

### III. FERTILITY IN THE TRIPLE HYBRIDS.

#### A. POLLEN FERTILITY.

In contrast to the primary hybrids, *turgidum*  $\times$  rye, which were completely sterile, some of the triple hybrids had dehiscing anthers and were partially pollen fertile. However, only those three triple hybrids which had exactly 42 chromosomes had dehiscing anthers, in the two plants with 41 and  $\pm 40$  chromosomes the anthers did not open, and therefore those plants were functionally completely male sterile. The five hybrids had been divided vegetatively into 15 clone plants. Clone plants from the same individual all behaved alike, those with 42 chromosomes producing good quantities of free pollen in contrast to the other plants, which lacked one or a few chromosomes. Only once was a small quantity of free pollen observed in an isolation bag on a clone plant with  $2n=41$ . — In the partially fertile plants with 42 chromosomes not all the anthers shed their pollen. The proportion between dehiscing and non-dehiscing anthers on these plants was evidently influenced by environmental conditions. On sunny days there was a marked increase in pollen production.

The pollen produced was partially sterile but contained a high proportion of good grains. According to table 3 the plants with  $2n=42$



had on the average 66,7 per cent good pollen (6 clone plants examined). In the plants with 41 and  $\pm 40$  chromosomes the non-dehiscing anthers were crushed and the quality of the pollen determined in the same way. In these plants the percentage of apparently good grains was lower, the average values being 53,0 in the clone plants with 41 chro-

TABLE 3. *Pollen fertility in the triple hybrids.*

Somatic chromosome number	Per cent good pollen grains								n	M
	10	20	30	40	50	60	70	80		
42						1	3	2	6	66,7
41				1	—	3	1		5	53,0
$\pm 40$		1	2	1					4	25,0

mosomes and only 25,0 per cent in those with  $2n = \pm 40$ . — Judging from this the anthers must contain a certain minimum percentage of good pollen grains in order to dehisce. In the present material and under the conditions given this value lies at about 60 per cent. — For

TABLE 4. *Pollen grain size.*

(Each unit in the table corresponds to  $1,84 \mu$ .)

Species or biotype	Pollen grain size																				n	M $\pm$ m	v
	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40			
<i>T. turgidum</i> , a	2	26	66	46	54	6															200	23,71 $\pm$ 0,08	4,7
» » b		3	9	30	56	55	39	7	—	1											200	25,68 $\pm$ 0,09	5,4
<i>T. vulgare</i> ...						5	19	26	34	51	33	22	10								200	29,72 $\pm$ 0,12	5,8
Triple hybrid, 2n = 41, a...	1	2	1	6	21	16	30	26	26	25	15	14	4	6	3	—	4				200	28,58 $\pm$ 0,21	10,3
Triple hybrid, 2n = 41, b...				4	11	15	18	29	17	39	21	21	7	3	2	—	—	—	1	2	190	29,30 $\pm$ 0,20	8,6
Triple hybrid, 2n = 42 .....		1	2	1	4	9	14	16	25	33	24	28	18	11	9	4	—	—	—	1	200	30,37 $\pm$ 0,20	9,2

control pollen quality was also examined in some samples from the parent species, *vulgare*, *turgidum* and rye. Six samples from three different *vulgare* biotypes (»Solvete III», »Kronvete» and »Drottivete») had all from 95 to 100 per cent good pollen. Three samples from *Triticum turgidum* gave the values 89, 94 and 95 but one sample from rye had only 68 per cent good pollen. — Six additional samples from

*Triticum dicoccum* and *monococcum* had all 96 to 100 per cent good pollen. Consequently, pollen fertility in the triple hybrids was lower than in the pure wheat species, both as regards quantity and quality.

Some measurements of pollen were undertaken which demonstrate that in the triple hybrids the size of the good pollen grains was more variable than in the pure species, *vulgare* and *turgidum* (table 4). Rye pollen was not available when the measurements were made. In the triple hybrids the coefficients of variation (v) vary between 8.8 and 10.3, in the pure species the corresponding values range from 4.7 to 5.8. This higher variation in the triple hybrids is no doubt due to irregularities at meiosis (cf. below) and formation of pollen grains with different chromosome numbers. Judging from the occurrence of occasional giant pollen grains a low percentage of unreduced male gametes were also formed by the triple hybrids. — The average pollen grain size in those hybrids was about the same as in *vulgare*, which was to be expected since the somatic chromosome numbers were the same or approximately the same.

#### B. FEMALE FERTILITY.

As part of the triple hybrids produced some rather good pollen it was considered possible to get self-fertilized progeny, and therefore practically all ears of the hybrids were isolated. Some seeds were also obtained but on the average seed setting was extremely poor. On the pollen fertile plants with 42 chromosomes a total of 52 ears were isolated and from those only 30 seeds were harvested, which seeds were considered to be capable or possibly capable of germination. The first vigorous shoots produced more grains than the weaker lateral shoots. Several grains were destroyed by insects, but anyhow the actual seed production was not higher than about one seed per ear.

The quality of grains obtained was quite variable and showed all transitions between large and well filled grains to small and shrivelled ones. Besides the seeds harvested a good many empty ones were also produced.

As expected the male sterile triple hybrids with 41 and  $\pm 40$  chromosomes did not produce a single seed in the isolation bags. A clone plant of the 41 chromosome hybrid produced a few seeds after pollination with *vulgare* pollen and thus proved to have functional ovules.

The seeds obtained from self-pollination of the triple hybrids have now been germinated. From the 30 seeds a total of 15 seedlings has been obtained. Nineteen seeds germinated but four of the seedlings

died early. From the seedlings root tips were fixed in order to determine the somatic chromosome numbers. In eight plants hitherto examined the chromosome numbers ranged from 39 to  $\pm 48$ . This variation in chromosome number is to be expected from the irregular meiosis in the mother plants.



Fig. 4. Somatic chromosomes of the triple hybrid ( $2n = 42$ ). —  $\times 2750$ .

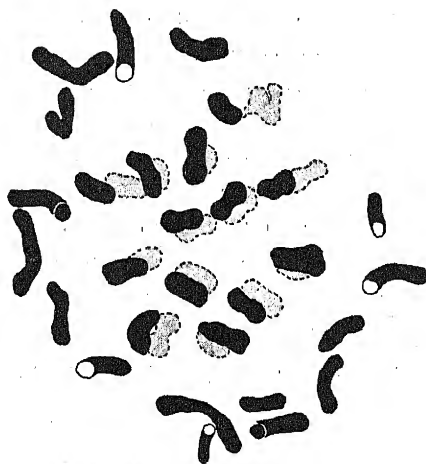


Fig. 5. Meiosis in the triple hybrid; I—M in polar view,  $13_{II} + 16_I$ . —  $\times 2970$ .

#### IV. MEIOTIC OBSERVATIONS.

In order to study meiosis in the triple hybrids smear preparations were made. The smears were fixed in chromacetic formalin and stained by gentian violet, and in this way some rather good slides were obtained.

To elucidate the interrelationships of the genomes of *vulgare*, *turgidum* and rye the chromosome configurations at first metaphase were examined. The present observations are limited to this important stage. A more complete account of meiosis in the triple hybrids may be given later on when the cytology of the primary hybrids, *turgidum*  $\times$  rye is better known. These hybrids are now being studied by Mr. A. LILJEFORS (cf. LILJEFORS 1935, in the press).

At first metaphase in the triple hybrids variable numbers of univalents, bivalents, trivalents and quadrivalents may be observed (figs. 5—8). Twentyfive complete metaphase groups, observed in side view, were analysed. The configurations found are summarized in table 5.

The most frequent configuration was  $14_{II} + 14_I$  (fig. 6) but quite often the number of univalents was higher and the number of bivalents proportionally lower. Fig. 5 represents a first metaphase in polar view with  $13_{II} + 16_I$ . Fourteen, however, is the most frequent number of univalents and occurred in 10 cells of 25, that is in 40 per cent of the cases. This may also be expressed in the following way. In 40 per cent of the cells 28 of the 42 chromosomes are united to bivalents, trivalents or quadrivalents, whereas the remaining 14 chromosomes appear as univalents.

TABLE 5. *Chromosome configurations in the triple hybrids.*

Configuration	Number of cells
$14_{II} + 14_I$	7
$13_{II} + 16_I$	3
$12_{II} + 18_I$	2
$11_{II} + 20_I$	1
$1_{IV} + 12_{II} + 14_I$	3
$1_{IV} + 11_{II} + 16_I$	2
$1_{III} + 13_{II} + 13_I$	1
$1_{III} + 12_{II} + 15_I$	4
$1_{III} + 11_{II} + 17_I$	2

The frequency of univalents in the 25 cells studied was the following:

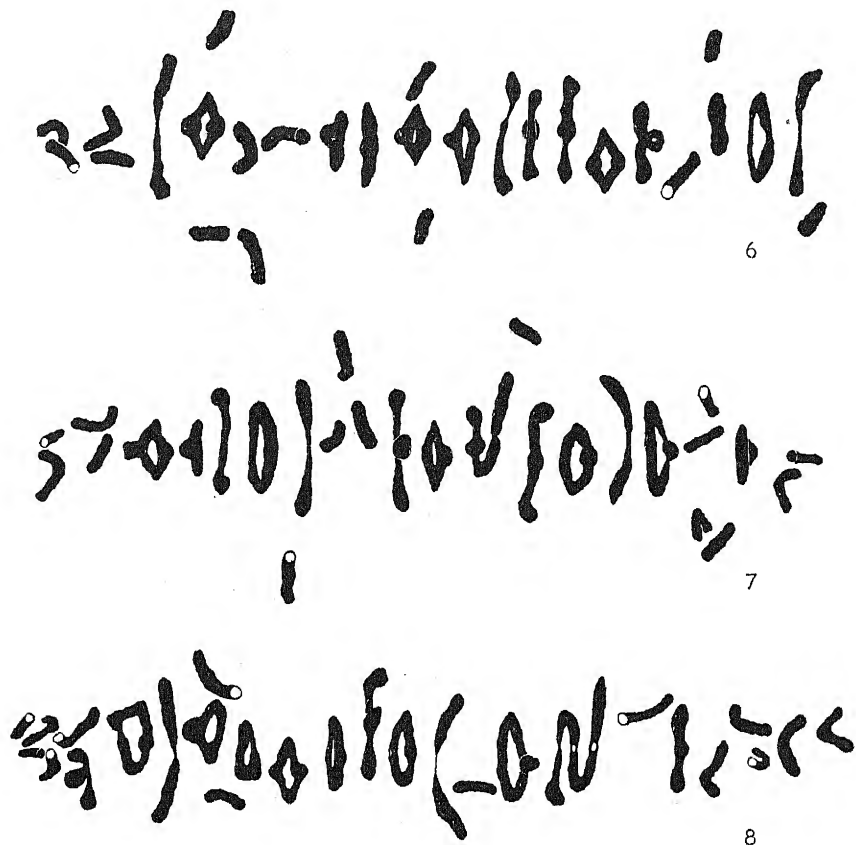
Number of univalents: ..	13	14	15	16	17	18	19	20
Frequency: .....	1	10	4	5	2	2	—	1

Fourteen is the commonest number but in more than half of the cells the number of univalents was higher. Only in one cell was the number lower.

In about half of the cells studied (12 of 25) either a trivalent or a quadrivalent was present. It is noteworthy that never more than one multivalent was present in the same cell and that this multivalent was either a trivalent or a quadrivalent. — The shape of the trivalents and quadrivalents was almost always the same, the former being V-shaped, as in fig. 7, the latter having the same zig-zag arrangement as in fig. 8.

The univalents were observed to differ in size considerably, but definite classification into big and small univalents seems to be impossible. — The bivalents were rod-shaped or ring-shaped, the number

of chiasmata ranging from one to three. Of 286 bivalents examined 125 were ring-shaped, 161 rod-shaped. This proportion is not absolutely accurate since it is sometimes difficult to distinguish the two types, but probably more than half of the bivalents are rod-shaped. Bivalents



Figs. 6—8. Meiosis in the triple hybrid (continued); I—M in side view (separately drawn but vertical position of the chromosomes unchanged). Fig. 6,  $14_{II} + 14_I$ ; fig. 7,  $1_{III} + 12_{II} + 15_I$ ; fig. 8,  $1_{IV} + 12_{II} + 14_I$  —  $\times 2960$ .

of this type, however, may be united by two chiasmata (cf. fig. 6, the fourth bivalent from the right).

Other meiotic stages in the triple hybrids than I—M have not been studied in detail, but univalents were observed to divide at I—A and lag at II—A. Micronuclei were seen at interphase and were frequent in the young tetrads, which as a rule consisted of four cells.

## V. DISCUSSION.

In the *turgidum*  $\times$  rye hybrids functional female gametes are formed, which contain the somatic chromosome number. It is highly probable that these gametes are unreduced and contain 14 *turgidum* + 7 rye chromosomes. If in species hybrids viable gametes with the somatic chromosome number are formed, these are usually regarded as unreduced, i. e. containing the complete genomes of both parent species. In most cases this assumption is no doubt correct, as has been demonstrated by numerous investigations of species hybrids and their polyploid progeny. — However, in the hybrid *Triticum durum*  $\times$  *monococcum* THOMPSON (1931) has observed the formation of restitution nuclei in the second division. Gametes formed in this way may have the somatic number but nevertheless they may not contain the complete genomes of both parents (l. c. p. 319).

Sterility was very pronounced in the *turgidum*  $\times$  rye hybrids. This fact alone strongly indicates that the few functional ovules really contain complete genomes, 14 *turgidum* + 7 rye chromosomes, and not for instance 16 *turgidum* + 5 rye chromosomes. — This view is further supported by the mode of chromosomes pairing in the triple hybrids. In hybrids between *Triticum vulgare* and *T. turgidum* 14 bivalents and 7 univalents is the typical I—M configuration. As demonstrated by numerous investigations (cf. WATKINS 1930) the bivalents are formed by the 14 *turgidum* chromosomes and 14 homologous *vulgare* chromosomes. In the triple hybrids the same number of bivalents was typical at first metaphase. This strongly indicates that the 14 *vulgare* chromosomes have also in this case found *turgidum* homologues. This being the case, the functional ovules with 21 chromosomes produced by the *turgidum*  $\times$  rye hybrids, have most probably carried 14 *turgidum* and 7 rye chromosomes. Consequently, the triple hybrids contain the complete genomes of rye, *turgidum* and *vulgare*. Seven rye and 14 *turgidum* chromosomes were brought together in the unreduced ovules of the primary hybrid and after crosses to *vulgare* these genomes were combined with the three *vulgare* genomes. — The genomic constitution of the resulting plants is also verified morphologically. The triple hybrids, no doubt, combine morphological characters from all of the three constituting species (p. 142 and figs. 1—3).

The occurrence of unreduced gametes in wheat crosses has already been demonstrated by several writers. In the cross *Aegilops ovata*  $\times$  *Triticum dicoccum* SAX (1928) found that all functional ovules were

unreduced and had 28 chromosomes. The *Aegilotriticum* type studied by KIHARA and KATAYAMA (1931) has probably arisen by the union of unreduced gametes. According to KOSTOFF (1932) functional unreduced ovules are formed by *T. dicoccum*  $\times$  *monococcum*  $F_1$  and such is the case also in *Triticum vulgare*  $\times$  rye hybrids (FLORELL 1931, PLOTNIKOWA 1934, KATTERMANN 1934).

The successful cross between a hybrid and a third species shows that in crosses between species with different chromosome numbers it may be better to cross the partially fertile hybrid to a third species rather than to the parent species. The gametic chromosome number of this third species should be the same as the chromosome number of the unreduced gametes of the hybrid. Even if such unreduced gametes are formed in rather low frequency they may be »picked up» by the gametes of the other parent and give viable, well balanced seeds which are capable of germination and further development.

In a previous paper (MÜNTZING 1933) a number of cases have been discussed, in which the union of gametes with the same or approximately the same chromosome number results in more viable zygotes than those which are formed by gametes with different chromosome numbers. — A new similar case in wheat is probably represented by the results of back crosses between *vulgare*  $\times$  rye hybrids and the parent species. In back crosses between *Triticum vulgare*  $\times$  rye,  $F_1$ , and *vulgare* more than half the functional ovules in the  $F_1$  hybrid are unreduced or approximately unreduced (cf. KATTERMANN 1934, Tabelle 5). However, in back crosses to rye studied by LEBEDEFF (LEBEDEFF 1932, according to KATTERMANN 1934) only about 20 per cent of the functional ovules had the somatic or approximately somatic chromosome number. As emphasized by KATTERMANN (l. c.) this gives the impression that *vulgare* pollen is chiefly suitable for those  $F_1$  ovules which have high chromosome numbers, in contrast to the rye pollen, which is better for the ovules with low chromosome numbers. — This result harmonizes very well with similar data from other material (cf. MÜNTZING 1933) and seems to demonstrate once more that the best zygotes are obtained from the union of gametes with the same or about the same chromosome number.

A triple wheat hybrid, obtained in the same way as the triple wheat—rye hybrids described in this paper, has been produced by KOSTOFF (1932). The hybrid *T. dicoccum*  $\times$  *monococcum* as female parent was pollinated with *T. vulgare*. The result was two hexaploid plants, which were triple hybrids, containing the sum of the chromo-

somes of *T. monococcum*, *dicoccum* and *vulgare*. The same cross, (*dicoccum*  $\times$  *monococcum*)  $\times$  *vulgare*, was repeated this summer by the present writer. Four well developed seeds were obtained after pollination of 7128  $F_1$  flowers with *vulgare* pollen. As the parent biotypes used were spring wheats these seeds have not yet been germinated, but they will probably give rise to new triple hybrids between *monococcum*, *dicoccum* and *vulgare*.

Another kind of triple hybrids was produced at the same time by pollinating *T. turgidum*  $\times$  *monococcum*  $F_1$  with *vulgare* pollen. In this cross five seeds were obtained from a total of 2254 flowers. In September, 1934, these seeds were germinated and gave four seedlings. A preliminary examination of the somatic chromosome numbers of those plants gave the following values:  $\pm 36$ , 42,  $\pm 42$  and  $\pm 44$ . Consequently, some of those plants represent hexaploid triple hybrids between *monococcum*, *turgidum* and *vulgare*.

Hybrids of a similar constitution have been produced by THOMPSON (1931). After open pollination of *turgidum*  $\times$  *monococcum* and *durum*  $\times$  *monococcum*,  $F_1$ , THOMPSON harvested some seeds, which gave a new generation. In this generation, » $F_2$ », the chromosome numbers were quite variable, but of the 41 plants examined nearly all had 28 or more chromosomes. Two daughter plants of *durum*  $\times$  *monococcum*,  $F_1$ , were hexaploid  $2n = 42$ . THOMPSON is of opinion that most of the grains set were the product of self-pollination and regards at least one of the hexaploids as only containing chromosomes from the diploid and tetraploid parent species. — However, as more than 98 per cent of the  $F_1$  pollen grains were shrunken and without contents (l. c. p. 311), it seems rather dubious that self-pollination could occur. When the pollen is so bad the anthers will probably not dehisce. In the *turgidum*  $\times$  *monococcum* plants studied by the present writer not a single anther was observed to dehisce, neither in the greenhouse nor in the experiment garden. Therefore it seems probable that all the  $F_2$  plants obtained by THOMPSON were really products of back crosses to other species. THOMPSON regards one of the hexaploids to be the result of out-crossing with some *vulgare* type and this plant may consequently represent a new kind of triple hybrid in wheat (*monococcum* + *durum* + *vulgare*).

From the examples discussed above it is evident that *almost any combination between diploid and tetraploid wheat species may give hexaploid triple hybrids when crossed to vulgare or other hexaploid*



wheat species. But not only diploid wheat species but also rye can be combined in the same way with tetraploid and hexaploid species.

As the rye + *turgidum* + *vulgare* hybrids were partially fertile and progeny after self-fertilization could be obtained it is probable that triple hybrids in which the rye genome has been substituted by a diploid wheat species will have equally good or better fertility. On account of the partial homology between e. g. the *monococcum* and *vulgare* genomes the triple hybrids *monococcum* + *turgidum* + *vulgare* will probably have a lower number of univalents at meiosis and hence a more regular chromosome distribution and better fertility.

The possibility of getting self-fertilized progeny from the triple hybrids opens new ways to obtain amphidiploids of various kinds. In our rye—*turgidum*—*vulgare* hybrids seven of the fourteen univalents are no doubt *vulgare* chromosomes, the remaining seven rye chromosomes. As in the hybrids the sterility was rather pronounced it is probable that gametes and zygotes containing complete genomes will be favoured. If that is the case a relatively high proportion of the gametes should carry 14 *turgidum* + 7 rye chromosomes and by union of such gametes an amphidiploid true-breeding *turgidum* + rye product should theoretically be produced. In the same way a *monococcum* + *dicoccum* amphidiploid or a *monococcum* + *turgidum* amphidiploid should be produced in the progeny from the corresponding triple hybrids. This would mean new primary material for plant breeding work.

Although in the rye—*turgidum*—*vulgare* hybrids fourteen was the most frequent number of univalents this number was higher in about 50 per cent of the cells, and as many as 20 univalents were observed in one cell. This may seem to indicate incomplete homology between the fourteen *turgidum* chromosomes, presumably derived from the *turgidum* × rye parent, and the corresponding chromosomes of *vulgare* (the A- and B-genomes). However, several cases in wheat are known in which the degree of pairing seems to be influenced also by other circumstances than chromosome homology.

In the  $F_1$  hybrid *Aegilotriticum* × *Triticum dicoccoides*, produced by KIHARA (1931),  $14_{II} + 14_I$  are to be expected at I—M since the *durum* genomes of *Aegilotriticum* are homologous to the *dicoccoides* genomes. However, the number of bivalents was found to be rather variable and ranged from 10 to 14. A similar unexpected decrease of pairing was observed by the same author also in *Aegilotriticum* × *Aegilops ovata*. — Hybrids between *Triticum vulgare* and rye often

form unreduced female gametes with 28 chromosomes. After back crosses to *vulgare* the resulting plants get 49 chromosomes, 42 of which are *vulgare* chromosomes, 7 rye chromosomes. Such plants should have  $21_{II} + 7_I$  but KATTERMANN (1934) observed that often more than seven univalents are formed. He suggests (l. c.) that this may be due either to dissimilarities between the *vulgare* genomes or »es gehen von den partnerlosen Roggenchromosomen Einflüsse aus, die die Paarung hindern«. In this connection the amphidiploid *vulgare*—rye hybrids should be remembered. Although in this case the rye chromosomes, as well as the *vulgare* chromosomes, have homologous partners, chromosome pairing is irregular and 2 to 6 univalents formed (LEVITSKY and BENETZKAJA 1929, 1931).

In other cases structural differences between the chromosomes may be responsible for the lack of pairing. In the pentaploid hybrid *Triticum durum*  $\times$  *vulgare*  $14_{II} + 7_I$  is the typical configuration, but sometimes  $13_{II} + 9_I$  are formed (KIHARA and NISHIYAMA 1930). According to VON BERG (1931 a) the number of bivalents in hybrids between tetraploid wheat species is often lower than 14. In the hybrid »*Aegilotriticum* II»  $\times$  *Triticum turgidovillosum* the same author (VON BERG 1931 b) could observe the mode of chromosome pairing between 14 chromosomes of *Aegilops ovata*, 14 of *Triticum durum*, 14 of *turgidum* and 7 of *T. villosum*, which chromosomes had all been combined in the  $F_1$  combination mentioned. As expected the typical number of univalents was 21 (*Aegilops ovata* + *T. villosum*) but was often higher. This was due to incomplete pairing between the *durum* and *turgidum* genomes. According to the author the number of bivalents also in *durum*  $\times$  *turgidum* hybrids is not always 14 but varies between 12 and 14. This is probably due to structural differences in some of the chromosomes, as DARLINGTON (1931) found a lower chiasma frequency in the hybrid *turgidum*  $\times$  *dicoccum* than in the parent species. — Finally it should be remembered that even in hybrids between different biotypes of *T. vulgare* chromosome pairing may be incomplete and univalents present (THOMPSON and ROBERTSON 1930, HOLLINGSHEAD 1932).

In view of the instances cited above the occasional lack of pairing in the triple hybrids between the *turgidum* chromosomes and their *vulgare*-homologues is not surprising, though it cannot be decided whether this is due to incomplete homology or to extra-chromosomal influences.

In the triple hybrids the majority of the chromosomes occurred

as bivalents or univalents but about 50 per cent of the p. m. c. also contained one trivalent or one quadrivalent. — Associations of more than two chromosomes are not unusual in wheat crosses and have been observed both in triploid, tetraploid and pentaploid wheat hybrids (KIHARA and NISHIYAMA 1930, YAMASHITA 1934) as well as in hybrids between *Triticum* and *Aegilops* (KIHARA and LILIENFELD 1932). According to KIHARA such associations arise as a result of complete or, more often, partial homology between chromosomes from different genomes or even from the same genome. KIHARA emphasizes the probable occurrence of structural changes, especially translocations, in *Triticum* as in many other genera. The chromosomes are therefore often partially homologous on account of the presence of homologous segments of different size and number. When such chromosomes are present in the same plant the result will often be associations of more than two chromosomes.

In the pentaploid hybrids between *Triticum durum* and *vulgare* KIHARA and NISHIYAMA (1930) observed a low frequency of trivalents which are considered to result from affinity between chromosomes belonging to the *B* and *D* genomes. According to KIHARA (1932) the diploid wheat species have the genomic constitution *AA*, the tetraploid species *AABB* and the hexaploid group *AABBDD*. Not only the *B* and *D* but also the *A* and *B* genomes are to a certain extent homologous. In the hybrids *T. dicoccum*  $\times$  *aegilopoides* and *dicoccum*  $\times$  *monococcum* KIHARA and NISHIYAMA (l. c.) found the typical configuration to be  $7_{II} + 7_I$  but of the bivalents as many as three might be changed to trivalents by addition of a corresponding number of univalents. This indicates a weak homology between the *A* and *B* genomes. — In plants from the back crosses (*vulgare*  $\times$  rye)  $\times$  *vulgare* KATTERMANN (1934) found multivalent associations, containing from three to six chromosomes, to be frequent. According to the author probably no rye chromosomes are members of these multivalents, which should thus be formed on account of homologies between chromosomes of different *vulgare* genomes.

As the investigations mentioned above demonstrate the existence of weak homologies at least between the *A* and *B* and the *B* and *D* genomes this may explain the occurrence of trivalents and quadrivalents in the triple hybrids. These hybrids contain two *A*, two *B* and one *D* genome in addition to the rye genome. However, as the frequency of quadrivalents was rather high in the triple hybrids (one quadrivalent in 20 per cent of the p. m. c.) and no quadrivalents were

observed by KIHARA and NISHIYAMA in the pentaploid hybrids, containing the same number of *A*, *B* and *D* genomes, it is possible that one rye chromosome is involved in the formation of the quadrivalents. Another possible cause is intragenomatic homologies caused by translocations.

For the solution of the problem the pairing conditions in the primary *turgidum*  $\times$  rye hybrids are of interest. LILJEFORS (1935, in the press) has studied the cytology of two different  $F_1$  combinations between *T. turgidum* and rye. In one of these there was almost complete asynesis, in the other  $F_1$  bivalents were not uncommon, the average number being 1.6. In the same  $F_1$  several trivalents and even a few quadrivalents were observed. For various reasons, cytological and genetical, LILJEFORS concludes that chromosome pairing in the *turgidum*  $\times$  rye hybrids is probably exclusively autosyndetic, though it cannot definitely be proved that no rye chromosomes pair with the wheat chromosomes. Unfortunately the triple hybrid, studied cytologically by the present writer, was the daughter plant of another  $F_1$  combination between *turgidum* and rye than those studied by LILJEFORS. Nevertheless his results strengthen the opinion that also in the triple hybrids the bivalents, trivalents and even quadrivalents are only formed by *turgidum* and *vulgare* chromosomes.

Also in the *vulgare*  $\times$  rye hybrids, studied by numerous workers, most of the chromosomes occur as univalents at meiosis, but generally a few bivalents are formed. According to Tabelle 1 in the paper by KATTERMANN (1934) the number of bivalents is, as a rule, 0—3 but may in exceptional cases be as high as 6. According to the same table BLEIER and KATTERMANN have also observed occasional trivalents. These associations in the *vulgare*  $\times$  rye hybrids are again, by most authors, regarded to be autosyndetic and to consist of *vulgare* chromosomes only. In any case the pairing conditions in *vulgare*  $\times$  rye,  $F_1$ , demonstrate that the rye genome is rather different from the wheat genomes.

Much cytogenetic work has been performed in order to elucidate the origin of the *vulgare* wheats, but no definite conclusions have been arrived at. It has been definitely demonstrated, however, that two of the three *vulgare* genomes, *A* and *B*, are homologous to the *A* and *B* genomes of the emmer group (cf. BLEIER 1930, THOMPSON 1931 b, KIHARA 1932). Concerning the origin of the third *vulgare* genome two main theories have been advanced (cf. SCHIEMANN 1932), those of PERCIVAL (1921) and MEISTER (1927). According to the first theory

the specific *vulgare* chromosomes are derived from the genus *Aegilops*. According to MEISTER the hexaploid wheat species have arisen from crosses between *dicoccum* and rye. PERCIVAL's theory has been supported by cytological observations, which clearly show that the third *vulgare* genome is homologous to one of the genomes of *Aegilops cylindrica*.

The rye hypothesis, on the other hand, is practically disproved by the meiotic behaviour of the *vulgare*  $\times$  rye hybrids. — The mode of chromosome pairing in the triple rye—*turgidum*—*vulgare* hybrids definitely shows that the *C* genome of *vulgare* (the *D* genome, according to the terminology of KIHARA) is not homologous to the rye genome. The typical configuration was here  $14_{II} + 14_I$  and only in one case out of twentyfive was the number of univalents lower than 14. Consequently, in the triple hybrids both the specific *vulgare* chromosomes and the rye chromosomes appear as univalents. The lack of pairing between these chromosomes strengthens the conclusion that the hexaploid wheat species have not arisen by crosses between rye and representatives of the emmer group.

### SUMMARY.

1) Hybrids between *Triticum turgidum* and rye were produced. These hybrids are highly sterile but a few unreduced, functional ovules are formed.

2) Crosses between *turgidum*  $\times$  rye,  $F_1$ , and *Triticum vulgare* resulted in five triple hybrids, which were hexaploid or approximately hexaploid.

3) The success of this cross is probably due to the fact that the unreduced ovules of  $F_1$  and the pollen grains of *vulgare* have the same chromosome number. In the same way other hexaploid triple hybrids may be obtained by crossing triploid wheat hybrids to *vulgare*.

4) The hexaploid (*turgidum*  $\times$  rye)  $\times$  *vulgare* hybrids were vigorous and partially fertile. Some progeny could be obtained after self-fertilization.

5) At first metaphase in the triple hybrids the most frequent chromosome configuration was  $14_{II} + 14_I$ , but the number of univalents was often higher. In about half of the cells one trivalent or one quadrivalent was present.

6) The chromosome associations demonstrate that the specific *vulgare* chromosomes are not homologous to the rye chromosomes.

This strengthens the conclusion that the *vulgare* wheats have not arisen by crosses between *Triticum dicoccum* and rye, as assumed by MEISTER.

Svalöf, Cyto-Genetic Department of the Swedish Seed Association, November 1934.

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# STUDIES ON THE INHERITANCE OF QUANTITATIVE CHARACTERS IN *PISUM*

## I. PRELIMINARY NOTE ON THE GENETICS OF TIME OF FLOWERING

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### GENERAL INTRODUCTION.

IN connection with the present author's investigations concerning varying linkage values for certain morphological factors in *Pisum* (RASMUSSEN 1927, 1934) a series of investigations on the inheritance of some quantitative characters was commenced. The main idea of those quantitative character investigations was to search for indications of their inheritance being influenced in the same manner as was observed for the morphological characters, i. e. showing different strengths of correlation when different parent lines were used for the crosses. The nature of the causes of the variation in linkage value for the same two factors may to some extent be elucidated by the knowledge of whether the crosses showing strong linkage between the morphological factors also show strong linkages between factors other than those first investigated. All the useful morphological factors in the material either belonging to one linkage group or being freely recombined made it desirable to look for linkages between quantitative factors and between those and morphological factors. Such linkages might be expected to throw some light on the causes of variation in linkage value. These considerations resulted in special interest being devoted to linkage between quantitative and morphological factors.

Although the above mentioned considerations were the main reasons for starting the investigations, it was fully realized that thorough quantitative investigations in a material which was from all angles very well known to the investigator and which, like the one at hand, gave the possibility of a series of interwoven crosses, might be of great use to our knowledge of quantitative inheritance and even give rise to new points of view in the theories of genetics.

When the first results were obtained and cursorily analysed it became evident that the complicated nature of the quantitative charac-



ters would make it rather difficult to bring out good evidence on the problems which were the primary cause for starting the series of investigations. On the other hand, it was obvious that the results could be reasonably expected to throw light on some other questions and, in fact, on questions which might finally be found to be more fundamental than the ones first in mind. One such question was that of the physiological co-operation between the cytoplasm and the genes of the nucleus. The consideration of that problem has already led the present author to formulate a tentative »interaction hypothesis» (RASMUSSEN 1933) which might as well have been named a general hypothesis of the inter-relation between genes and the reaction of the cytoplasm to them. Further, SIRKS' (1929) and others' attempt to explain the quantitative inheritance phenomena as being caused by series of allelomorphs with frequent mutation made it desirable to try to demonstrate proper polygenic inheritance in quantitative characters, even if the allelomorph theory in itself did not fit in well with our general experience of, for instance, mutation rates. Later on the questions of the evolution of dominance have attracted considerable interest since FISHER (1928) published his ideas on this problem. It may also be pointed out that the mere knowledge of the strength of the dominance in a number of quantity genes will be of value as well for the practical breeding work as for the theory of inbreeding.

The desire to arrive at as full evidence as can reasonably be expected together with the necessity for a thorough consideration of the results in the author's mind and the necessity to learn enough statistics to be able to handle the quantitative problems in an adequate way, has caused withholding of publication of the results, although the main part of the experimental work was finished in 1930.

In general the following system of publication will be adopted: to each of the quantitative characters studied will be devoted a special paper in which will also be included its relations to certain morphological characters. When the single characters have been treated it is intended to publish the results concerning their genic inter-relations.

The writer takes this opportunity to express his sincere thanks to several persons and institutions who have aided him in many ways in carrying through the research work, viz. to Professor H. NILSSON-EHLE for discussion of the work and the results and for valuable advice and suggestions, as well as for placing at my disposal the facilities of the Institute of Genetics of the Lund University; to my former chief, Mr. C. G. DAHL of Alnarp, where the work was begun,

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### REVIEW OF PREVIOUS WORK ON THE INHERITANCE OF TIME OF FLOWERING IN *PISUM*.

Already in the early days of modern genetics the flowering time of the pea evoked the interest of investigators (HOSHINO, 1915; LOCK, 1904; TSCHERMAK, 1902). Later investigators have attempted to add further to our knowledge of this matter. Had it not been for the special problems which in this case are connected with the flowering time the present author would scarcely have contemplated adding one more name to the long list of workers in this special field. In spite of considerable labour expended in the study of the genetics of flowering time in *Pisum* there still prevails some uncertainty as to the proper genic interpretation of the results. This situation makes it necessary to give a short review of the results of previous research work as well as an otherwise unnecessarily detailed account of the present writer's own of the segregation figures.

✓ Flowering time in *Pisum* is closely connected with the number of the first flowering internode. Both characters are, however, determined by several factors and the correlation between them is far from absolute (WELLENSIEK 1925). Therefore, the relations between them must be treated in a special paper after the inheritance of the internode number has been published.

MENDEL (1865) already made some observations on the inheritance of flowering time but naturally found the character to be too complicated for use in his fundamental experiments.

TSCHERMAK (1902) was the first after 1900 to start the investigation of the flowering time in *Pisum*, his first publication demonstrating that this character showed segregation in 1 of crosses, which was a point of special interest at that (1910) he published the result of continued investigation the flowering time and tried to formulate distinct factors the time of flowering. From a compound of sev. different parents, he drew the following conclusion

basis of the flowering time: *A*-factor giving intermediate flowering time tending towards late, *B*-factor, inactive without *A*, shortening the time determined by *A*. His evidence does not, however, seem very convincing, partly because of small progenies and partly because the conclusions are drawn by compounding offspring of different crosses. He further stated that there was a correlation between flower colour and time of flowering, the purple factor being correlated with late flowering. In addition to his own conclusions, it may be mentioned that TSCHERMAK's material rather obviously suggests the existence of several modifying factors.

LOCK (1904, 1905, 1907) obtained results which seem to indicate the segregation of several flowering time factors and he concludes himself (1907) that, at that time, nothing was known about the heredity of flowering time in *Pisum*. He has, however, noted the relation between flower colour and time of flowering.

KEEBLE and PELLEW (1910) recorded, after a cross between a very early and a very late variety, a segregation spreading from the flowering time of the early parent nearly to that of the late parent. They interpreted their results as showing the effects of one gene pair with prevalence of lateness. They further concluded that this only accounted for part of the segregation and then left the problem at that. They also noted a rather strong correlation between late flowering and thick internodes, interpreting the results in terms of linkage with a recombination value of 12.5 %.

HOSHINO (1915) reported an extensive series of investigations on this subject, including data from  $F_3$  and  $F_4$ . He arrived at the conclusion that the flowering time is determined by two factors *A* and *B* but differs from TSCHERMAK (l. c.) in the effects ascribed to these factors. HOSHINO defines them as follows: *A* gives late flowering, *B*, hypostatic to *A*, gives early flowering. Because of not finding a clean cut segregation giving the several types to be expected on his factor scheme, he concludes that the genes have been contaminated in the cross. There can, however, be no doubt that the overlapping in one of the  $F_3$ - and  $F_4$ -types is due to the segregation of factors. He also notes a correlation between purple flowers and late flowering and interprets this as a result of a linkage between the purple factor and the late flowering factor. He even mentions giving a gametic series of 7 : 1.

(1925) arrived at the conclusion that two factors determine flowering time in the cross investigated by him:

i. e.  $I_f'$  — intermediate flowering ( $i_f'$  — early flowering) and  $L_f'$  retards flowering caused by  $I_f'$ , in itself inactive. The distribution of flowering time in  $F_2$  gave, however, a normal distribution curve. The two factor hypothesis was arrived at after an arbitrary dividing of the  $F_2$ -plants into groups which did not show any distinct differentiation.

WHITE (1917) and WELLENSIEK (1925) have both reviewed the results of earlier research work concerning the flowering time in *Pisum*. WHITE mainly refers the results and conclusions arrived at before 1917 but he draws attention to the fact that in several crosses, constant types which flower earlier and later than either parent have been isolated and his whole attitude seems to convey, as his impression, that we have not so far got at the whole truth of the matter. WELLENSIEK makes an attempt to bring the rather contradictory results into agreement but finally gives it up.

One thing seems, however, to be definitely proved by the previous investigations on flowering time, i. e. that there is a connection between flowering time and flower colour. There is also evidence for a connection between flowering time and type of internodes, although there remains some doubt about which internode factor is concerned. This should mean that two factors of marked effect govern the flowering time. In any specific cross neither, one or both of them may segregate. The difficulties arising in the ascertaining of what is happening in any single case may be due to the simultaneous segregation of a number of modifying genes. Indications of this being the case are to be found in the material published by the investigators referred to above. In these circumstances the main points to be elucidated as regards the flowering time proper are: 1) can two or more distinct genes be traced? 2) what is the effect of each of them and do their heterozygotes show dominance? 3) to what degree is the flowering time governed by the main genes and to which degree by modifiers? Before the main questions mentioned in the introduction to this paper can be approached the questions above need careful consideration. They will therefore be treated first.

## METHODS.

The methods of cultivation have on the whole been the same as those described in the writer's paper on changing linkage values (RASMUSSEN 1927) and need not be repeated here.

The methods of observation have been somewhat different

different cases. In the  $F_1$ - and  $F_2$ -progenies the following procedure has mostly been applied. Each plant was labelled and numbered and each day, after the first flowers appeared, the plot was examined, the date of flowering for each plant being noted in lists. The morphological characters were generally scored on the mature plants in the winter time. In some cases the same methods were used for determining the flowering time of the parent lines.

The great number of plants in  $F_3$  and following generations necessitated adopting another system, i. e. counting of the number of flowering plants in each plot either every day or every second day. At the end of the flowering period the intervals were generally made longer. In the cases where this procedure was used no connection between the flowering time and the other characteristics of the single plant could be established. When 75 % of the plants were flowering it was found to be difficult to count, with accuracy, the number of flowering plants. Therefore, when this point was reached or passed, the plot was characterized as being in full flower (marked »F«).

Throughout the work, plants showing signs of having been damaged in any way have been excluded.

The flowering time was defined as the number of days from sowing to the appearance of the first flower with the standard nearly flattened out. The actual number of days is not, however, used as the measure of the flowering time. The whole crop of peas varies from the one year to the other because of weather and cultivation conditions. It would be highly undesirable to have to trouble with that variation as well as the other variation in the material. Therefore, a relative measure has been made use of. Certain parent lines were grown every year, and their average date of flowering in any year was used as the point from which flowering times, in that year, were measured. That average date has been called 0 (zero) and the flowering time of plants and plots have been determined as deviations from the 0-value, all comparisons of this kind, naturally, being made within each year.

For the calculation of the statistics FISHER's (1934) methods and symbols have, in general, been used. The most important symbols are thus:

$\bar{x}$  = mean,

var = variance =  $s^2$ ,

$s$  = standard deviation,

s. e. = standard error of mean,

$S$  = summation.

The cases where the flowering time has been determined only up to the day of 75 % flowering need special attention. Also the modification curve of flowering time in pure lines hints at the straightforward methods not being quite adequate. Therefore, other methods of calculating mean and variation measures have been adopted for some cases.

The variation in flowering time in pure lines is to be seen in table 1. In most cases the number of flowering plants suddenly rises so that most of the plants flower 4—5 days after the first flowers appear. After about 90 % of the plants have flowered a very long time may elapse, before the last one comes on, if it ever does arrive at flowering. On some occasions those very late flowering plants were

TABLE 1. *Percentage of plants in bloom on different dates.  
Pure lines 1926.*

Line	Date																								
	June							July																	
	24	25	26	27	28	29	30	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	
Gj.....													1		40		72	82		84		91			
WW...				1	2	9		62	91			98		99		100									
Es II													13		46		72	87		89		98			
St.....										1		32		51	56		71	78		88		94			
Bism	2	5	7		62		76		84	85	90	91	95				99	100							
Gd ...											11	37		85	91		94	97		98		99			

more carefully observed and all of them were found to be damaged in the early stages or to have come from occasionally late germinating seeds. This makes them fall outside the biologically normal variation and they should naturally be excluded from the account. This has been done by using, instead of the arithmetic mean, the time the flowering curve passes the 50 % point, as the characteristic of the group, i. e., the mode instead of the mean is used in these cases. The standard deviation as a measure of the size of the variation is, under the circumstances, no quite adequate measure. Still it is the best simple measure available and therefore has been made use of in the cases where the observations allow of calculation. The time between the 25 % and the 75 % points of the flowering curve has, however, in some cases been used for estimating the size of the variation. This gives in fact the quartile of a normal distribution. Although the distribution of the flowering time is not normal, we can arrive

at a rough estimate of the standard deviation by multiplying (difference 25—75 % point)  $\times 0,6745$ . When an estimate of the standard deviation is needed in the cases where the scoring of the flowering stopped at 75 % flowering plants, this method must be used.

### THE MATERIAL.

The original material used in the investigations was the pure lines of different pea varieties employed in the author's 1927-paper, i. e.:

	Average flowering time 1926—1933
Gj : <i>Le P v A R I</i> .....	+ 8,8
EsII : <i>Le p v a R I</i> .....	+ 2,5
St : <i>Le P V a r I</i> .....	+ 3,4
Bism : <i>Le p V a R I</i> .....	— 6,1
WW : <i>le Cry<sub>1</sub> cry<sub>2</sub> P V a r i</i> .....	— 1,3
Gd : <i>le cry<sub>1</sub> cry<sub>2</sub> p v A R I</i> .....	+ 3,5
Buxb : <i>le P V a R I</i> .....	— 8,3

The flowering time was investigated in the following crosses between these lines:

Gj  $\times$  WW  
 St  $\times$  Gd  
 Gj  $\times$  Bism  
 Gj  $\times$  EsII  
 EsII  $\times$  Buxb  
 Bism  $\times$  Buxb  
 Bism  $\times$  Gd  
 WW  $\times$  Gd

In all these cases the flowering time of the individual  $F_2$ -plants was noted and a great part of the material, especially from Gj  $\times$  WW, St  $\times$  Gd, EsII  $\times$  Buxb, was followed in  $F_3$  to  $F_5$ . Selection was further carried out in order to procure constant early flowering purple (A) types as well of tall (*Le*) as of dwarfs (*le*). Such types were also extracted from the crosses Gj  $\times$  Bism («HRT II» — tall), Gj  $\times$  WW («HRT I» — tall, «LRT I» — dwarf) and Gd  $\times$  Bism («LRT II» — dwarf). Those early segregation types were again used for crosses with the original lines in 1930 — of material grown in 1933. The flowering time and the genic constitution of these lines are the two most important genes, i. e. A (flower colour) and T (internode length) of the extracted

segregates are to be seen in table 2. In that table the flowering times in 1933 of the parent varieties concerned are presented for comparison.

It might be noted now that from the cross  $Gj \times WW$ , where the early flowering parent is not extremely early, it has been possible to isolate two transgressive types, both flowering about three days earlier than the early parent type.

TABLE 2. *Flowering times in 1933 of parent varieties and segregates and genic formulae of later.*

Parent I		Segregate types ( $F_6$ )			Parent II	
Symbol	Flowering time	Symbol	Flowering time	Genic formula	Symbol	Flowering time
Gj .....	+8,5	LRT I	-4,73	<i>le A</i>	WW	-1,3
Gd .....	+3,5	LRT II	-7,90	<i>le A</i>	Bism	-9,3
Gj .....	+8,5	HRT I	(-4)	<i>Le A</i>	WW	-1,3
Gj .....	+8,5	HRT II	-6,06	<i>Le A</i>	Bism	-9,3

The following crosses were made with the segregate types:

$LRT II \times St$   
 $\quad \times EsII$   
 $LRT I \times WW$   
 $LRT II \times WW$   
 $HRT II \times Gd$   
 $\quad \times Bism$   
 $\quad \times St$   
 $HRT I \times EsII$

In these crosses only the flowering time of  $F_2$  has been investigated.

## THE RESULTS.

Although it has been necessary to go into some details in describing the scope and methods of the investigation only the most important results will be given here.

The main results of the  $F_2$ -segregations are presented in table 3. Before beginning to analyse them some facts must be mentioned concerning the distributions,  $F_3$ -results and so on.

The  $F_2$ -distribution of flowering time is in most cases very



from normal. It is often skew with the individuals massing at the late end of the curve. This is in contrast to the distributions of the pure lines which also often show skewness but in the other direction, i. e. with the individuals gathering towards the early end. The  $F_2$ -distributions also deviate from the normal variation curve by being highly excessive or rather containing many summits. The comparison of  $F_2$  and  $F_3$  has clearly demonstrated that the later abnormality of

TABLE 3. *Summary of flowering*

Parents	Flowering time of parents						Flow	
							Le	
	$\bar{x}$	$\pm m$	var	$\bar{x}$	$\pm m$	var	$\bar{x}$	$\pm m$
Gj ( <i>Le A</i> ) $\times$ WW ( <i>le a</i> ) .....	+6,3	$\pm 0,24$	4,27	-1,1	$\pm 0,19$	4,92	+2,11	$\pm 0,278$
St ( <i>Le a</i> ) $\times$ Gd ( <i>le A</i> ) .....	+4,9	$\pm 0,44$	13,34	+4,5	$\pm 0,35$	12,74	+3,10	$\pm 0,13$
Gj ( <i>Le A</i> ) $\times$ Bism ( <i>Le a</i> ) .....	+6,0	$\pm 0,24$	4,27	-4,6	$\pm 0,25$	7,37	—	—
Gj ( <i>Le A</i> ) $\times$ EsII ( <i>Le a</i> ) .....	+6,0	$\pm 0,24$	4,27	+5,8	$\pm 0,18$	5,92	—	—
EsII ( <i>Le a</i> ) $\times$ Buxb ( <i>le a</i> ) .....	+5,8	$\pm 0,18$	5,92	(-7,7)			-1,13	$\pm 0,42$
Bism ( <i>Le a</i> ) $\times$ Buxb ( <i>le a</i> ) .....	-4,6	$\pm 0,25$	7,37	(-7,7)			-6,83	$\pm 0,39$
Bism ( <i>Le a</i> ) $\times$ Gd ( <i>le A</i> ) .....	-4,6	$\pm 0,25$	7,37	+4,5	$\pm 0,35$	12,74	-1,04	$\pm 0,36$
WW ( <i>le a</i> ) $\times$ Gd ( <i>le A</i> ) .....	-1,1	$\pm 0,19$	4,92	+4,5	$\pm 0,35$	12,74	—	—
LRT II ( <i>le A</i> ) $\times$ St ( <i>Le a</i> ) .....	-7,90	$\pm 0,27$	8,99	+3,73	$\pm 0,24$	4,29	+3,88	$\pm 0,30$
LRT II ( <i>le A</i> ) $\times$ Es II ( <i>Le a</i> ) .....	-7,90	$\pm 0,27$	8,99	+3,73	$\pm 0,39$	2,71	-1,58	$\pm 0,79$
LRT I ( <i>le A</i> ) $\times$ WW ( <i>le a</i> ) .....	-4,73	$\pm 0,41$	9,06	(-1,3)			—	—
LRT II ( <i>le A</i> ) $\times$ WW ( <i>le a</i> ) .....	-7,90	$\pm 0,27$	8,99	(-1,3)			—	—
LRT II ( <i>le A</i> ) $\times$ Gd ( <i>le A</i> ) .....	-7,90	$\pm 0,27$	8,99	(+3,5)			—	—
HRT II ( <i>Le A</i> ) $\times$ Gd ( <i>le A</i> ) .....	-8,72	$\pm 0,30$	10,25	(+3,5)			-4,00	$\pm 0,65$
HRT II ( <i>Le A</i> ) $\times$ Bism ( <i>Le a</i> ) .....	-8,72	$\pm 0,30$	10,25	(-9,3)			—	—
HRT II ( <i>Le A</i> ) $\times$ St ( <i>Le a</i> ) .....	-8,72	$\pm 0,30$	10,25	+3,73	$\pm 0,24$	4,29	—	—
HRT I ( <i>Le A</i> ) $\times$ Es II ( <i>Le a</i> ) .....	(-5)		—	+3,73	$\pm 0,39$	2,71	—	—

the curve is due to genic segregation as well as to the weather conditions producing an uneven flowering. The last mentioned fact makes it difficult, if not impossible, to use the  $F_2$ -distribution for tracing individual flowering time genes.

The comparison between  $F_2$  and  $F_3$  has been made in some cases. The total correlation between  $F_2$  and  $F_3$  is not very high (about 0,5) but its most prominent feature is a marked tendency to show curved regression lines, with good correlation in the early flowering part of the field and lack of correlation in the late part. When only those families which show a variation in flowering time of about the

same size as the pure lines are compared with their  $F_2$ -parents somewhat more normal correlations are obtained but the tendency to lack of covariance in the late part of the field is still prominent. These results indicate that the flowering time of the individual  $F_2$ -plant is mainly determined by its genic constitution and that the environmental conditions have only played a minor part. The skewness of the curves further indicates that the dominance should lie towards the late side.

*time of  $F_2$  from different crosses.*

er ing time of $F_2$										Total		
<i>Le</i>	<i>le</i>			<i>A</i>			$\alpha$					
var	$\bar{x}$	$\pm m$	var	$\bar{x}$	$\pm m$	var	$\bar{x}$	$\pm m$	var	$\bar{x}$	$\pm m$	var
13,88	+4,84	$\pm 0,39$	10,75	4,05	$\pm 0,231$	10,01	-0,64	$\pm 0,43$	11,42	+2,85	$\pm 0,27$	18,56
6,93	+4,65	$\pm 0,23$	6,47	+3,60	$\pm 0,14$	7,58	+3,39	$\pm 0,23$	7,04	+3,54	$\pm 0,12$	7,43
—	—	—	—	+5,37	$\pm 0,31$	15,46	+2,11	$\pm 0,76$	27,28	+4,83	$\pm 0,31$	19,92
—	—	—	—	+5,44	$\pm 0,31$	7,92	+5,23	$\pm 0,52$	8,17	+5,42	$\pm 0,26$	7,98
21,33	+2,55	$\pm 0,71$	20,35	—	—	—	—	—	—	-0,24	$\pm 0,38$	23,56
7,90	-2,37	$\pm 0,96$	28,74	—	—	—	—	—	—	-5,19	$\pm 0,48$	18,95
13,80	+0,46	$\pm 0,55$	13,25	+0,54	$\pm 0,17$	8,11	-3,85	$\pm 0,59$	13,72	-0,58	$\pm 0,29$	13,26
—	—	—	—	+0,62	$\pm 0,16$	6,34	-1,49	$\pm 0,38$	8,80	+0,44	$\pm 0,16$	7,74
6,48	+6,05	$\pm 0,68$	9,63	+4,86	$\pm 0,32$	7,21	+3,02	$\pm 0,56$	7,80	+4,37	$\pm 0,29$	7,72
22,5	+2,60	$\pm 2,20$	29,1	-1,49	$\pm 1,05$	29,8	+1,67	$\pm 0,61$	2,62	-0,84	$\pm 0,98$	25,5
—	—	—	—	-5,52	$\pm 0,24$	7,28	-4,86	$\pm 0,50$	10,90	-5,43	$\pm 0,22$	8,13
—	—	—	—	-7,0	$\pm 0,30$	9,8	-8,40	$\pm 0,62$	10,89	-7,56	$\pm 0,17$	—
—	—	—	—	—	—	—	—	—	—	-3,16	$\pm 0,26$	10,74
13,0	-2,15	$\pm 1,15$	15,8	—	—	—	—	—	—	-3,48	$\pm 0,57$	13,8
—	—	—	—	-7,97	$\pm 0,36$	5,66	-8,30	$\pm 0,81$	6,49	-8,03	$\pm 0,32$	5,71
—	—	—	—	-1,24	$\pm 0,20$	12,32	+1,63	$\pm 0,23$	3,03	-0,72	$\pm 0,16$	10,04
—	—	—	—	-1,38	$\pm 0,31$	10,55	+2,79	$\pm 0,31$	4,77	-0,48	$\pm 0,28$	16,1

If dominance cannot account for all the skewness there is also an indication of an interaction between the flowering time genes, resulting in the late ones becoming less and less effective as they are piled up together. These indications are further emphasized by the fact that the modification curves of the pure lines are generally skew in the opposite direction.

Table 3 clearly demonstrates that the flowering time is partly determined by two main genes connected with respectively the *Le*- and the *A*-factor. The one connected with the *A*-factor (purple flower versus white) is the easier to deal with.

## A-FACTOR AND FLOWERING TIME.

Table 4 shows the difference in flowering time between the parents and between different types segregating in  $F_2$  and demonstrates the distribution of genes  $A$ — $a$ ,  $X_a$  and  $x_a$  in the material.

TABLE 4. Differences in flowering time between parents and different  $F_2$  types concerning factors  $A$ ,  $a$ ,  $X_a$  and  $x_a$ .

Difference in flowering time in days				
Parents				$F_2$
Lines	Genotypes	$A$ minus $a$	$X_a$ minus $x_a$	$A$ minus $a$
Gj $\times$ WW .....	$A X_a \times a x_a$	+ 7,1	+ 7,1	+ 4,69
St $\times$ Gd .....	$a X_a \times A X_a$	+ 0,4	—	+ 0,11
Gj $\times$ Bism .....	$A X_a \times a x_a$	+ 10,6	+ 10,6	+ 3,26
Gj $\times$ Es II .....	$A X_a \times A X_a$	+ 0,8	—	+ 0,21
Bism $\times$ Gd .....	$a x_a \times A X_a$	+ 9,1	+ 9,1	+ 4,39
WW $\times$ Gd .....	$a x_a \times A X_a$	+ 5,6	+ 5,6	+ 2,41
LRT II $\times$ St .....	$A x_a \times a X_a$	— 11,2	+ 11,2	+ 1,64
LRT II $\times$ Es II ...	$A x_a \times a X_a$	— 11,2	+ 11,2	— 3,16
LRT I $\times$ WW .....	$A x_a \times a x_a$	— 3,4	—	— 0,66
LRT $\times$ WW .....	$A x_a \times a x_a$	— 6,6	—	+ 1,40
HRT II $\times$ Bism .....	$A x_a \times a x_a$	+ 0,6	—	+ 0,33
HRT II $\times$ St .....	$A x_a \times A X_a$	— 12,5	+ 12,5	— 2,87
HRT I $\times$ Es II .....	$A x_a \times A X_a$	(— 8,9)	(+ 8,9)	— 1,41

The upper part of table 4 contains the pure line crosses. These obviously show that there is one factor, having a rather strong effect linked with the  $A$ -factor. We might name it  $X_a$ . Gj, St, Gd, and EsII are  $X_a$ , and WW and Bism  $x_a$ . The average effect of the  $X_a$  when full dominance is assumed should be to retard flowering about 3 days. This fits in with the results of previous investigators mentioned in the introduction. However, it can be demonstrated that the factor in question is not absolutely dominant. In the cross Gj  $\times$  WW several  $F_2$ -plants chosen at random were tested in  $F_3$ . Among these the  $Aa$ -types can be picked out of the  $A$ -phenotypes. The flowering times of the three groups came out as follows:

$aa$ .....	+ 0,04
$Aa$ .....	+ 3,7
$AA$ .....	+ 5,2

Not taking into account the crossing over between  $A$  and  $X_a$  this would mean a prevalence for  $X_a$  over  $x_a$  of about 70 %. All facts point towards a rather strong linkage and we shall therefore not be much mistaken if we assume the effect of one  $X_a$  to be only slightly stronger than indicated by the difference  $A$ — $a$ -types. The assumption of one  $X_a$  having an effect = 80 % of two  $X_a$ 's seems to come rather near the truth.

The difference between  $A$ - and  $a$ -types varies in the  $F_2$ -progenies of pure line crosses of table 4 from + 4.69 to + 2.41 in those cases where  $X_a$ — $x_a$  is segregating. Random sampling will be responsible for this variation to a rather great extent. Still, other agents might be among the causes too. Thus different strengths of linkage between  $A$  and  $X_a$  would produce such differences. Whether differences in linkage value also play a prominent role here cannot, however, be decided now.

Previous investigators working on the correlation between flower colour and flowering time have contented themselves with investigating the  $F_2$ . The exception is HOSHINO (l. c.) who went as far as to  $F_4$ . Since it is still of great importance in quantitative genetics to be absolutely sure of one's ground where linkages are concerned, it was deemed necessary to put the linkage between  $A$  and  $X_a$  to the crucial test. This was done by extracting the early flowering  $A$ -segregates and working some crosses between them and the parent types. The sum impression of the results from these crosses, presented in the lower half of table 4, is that all the extracted types have got the  $x_a$ -factor, since on the whole the crosses between early purple and white-flowering  $X_a$ -lines show the purples coming out as the earlier type in  $F_2$ . LRT II  $\times$  St and WW cause a little trouble in this respect but in both cases the standard error is rather great and, more important, the LRT II was evidently not homozygous in  $F_4$  where the crosses were made. Thus it is probable that not all cross-fertilisations with LRT II have been crosses with  $x_a$ . We might thus neglect those exceptional cases and conclude that a typical linkage between  $A$  and  $X_a$  has been established, the early flowering purple segregates resulting from recombination of the genes  $A$  and  $X_a$ .

#### Le-FACTOR AND FLOWERING TIME.

As is to be seen from table 3 the  $Le$ -factor also influences the flowering time of the segregates. Table 5 presents the differences between the parents and between  $Le$ — $le$ -types in  $F_2$ . From table 5 it can be seen that the parental combination of  $Le$

and flowering time has practically no influence at all on the result of the cross. Whether the tall parent is early or late the tall segregates flower, on the average, earlier than the dwarfs. This is in striking contrast to the case of the *A*-factor and flowering time. The effect of the *Le*-factor on time of flowering being undisputable we have the choice between assuming *Le* to have a pleiotropic effect on flowering time or a very strong linkage between *Le* and a hypothetical flowering time factor. The data known do not now allow of a crucial test as to which of the two assumptions is the right one but the evidence seems

TABLE 5. *Difference in flowering time between Le- and le-parents and between Le- and le-types in F<sub>2</sub>.*

Cross	Difference in days <i>Le</i> -type minus <i>le</i> -type	
	Parents	<i>F</i> <sub>2</sub>
Gj × WW ( <i>Le</i> × <i>le</i> ) .....	— 7,1	— 2,73
St × Gd ( <i>Le</i> × <i>le</i> ).....	— 0,4	— 1,55
EsII × Buxb ( <i>Le</i> × <i>le</i> ) .....	— 13,3	— 3,68
Bism × Buxb ( <i>Le</i> × <i>le</i> ).....	— 3,1	— 4,46
Bism × Gd ( <i>Le</i> × <i>le</i> ).....	— 9,1	— 1,50
LRTII × St ( <i>le</i> × <i>Le</i> ).....	+ 11,2	— 2,17
» × EsII ( <i>le</i> × <i>Le</i> ) .....	+ 11,2	— 4,18
HRTII × Gd ( <i>le</i> × <i>Le</i> ) .....	+ 12,2	— 1,85

rather in favour of the pleiotropy, therefore the *Le*-factor may be taken as a flowering time factor as well as an internode length factor.

The three internode genotypes give the following flowering times in *F*<sub>2</sub> of Gj × WW:

<i>Le Le</i> .....	+ 1,8
<i>Le le</i> .....	+ 4,0
<i>le le</i> .....	+ 4,5

From this it can be seen that one *le* retards the flowering time in this cross by 2,2 days and that the addition of one more *le* makes a further retardation of 0,5 days. So it is evident that the *le* recessive for internode length is dominant for flowering time with about 80 % prevalence.

The variation in effect of the *le*-factor needs special consideration, which it will receive in a subsequent part.

THE AMOUNT OF VARIATION IN FLOWERING TIME CAUSED BY  
DIFFERENT AGENTS.

An analysis of the variation of flowering time in  $F_2$  of Gj  $\times$  WW has been attempted. The total sum of squares is 4695. From this can first be subtracted the variation belonging to four morphological groups tall—purple, tall—white, dwarf—purple and dwarf—white since the average effect of these morphological combinations on the flowering time is known. This is done from the formula (in FISHER's symbols):

$$\begin{aligned} S(x - \bar{x})^2 = & n_{p_1}(\bar{x}_{p_1} - \bar{x})^2 + n_{p_2}(\bar{x}_{p_2} - \bar{x})^2 + S(x_{p_1} - x_{p_1})^2 + \\ & + S(x_{p_2} - \bar{x}_{p_2})^2 + \dots \end{aligned}$$

(The reason for not taking each morphological factor by itself is that their effects on flowering time show interaction, as will be demonstrated below.) The sum of squares due to the two main flowering time factors is = 1479. This gives:

	Sum of squares	Degrees of freedom
Total .....	4695	253
Main factors .....	1479	3
Residual = external and genic modifiers	3425	250

From this is to be seen that about one third of the variation in  $F_2$  is caused by the two main factors and two thirds are left to be divided between environmental modification and genic influences other than that of the two main factors. We might get an estimate, although a very rough one, of the size of the variation caused by environment from the variation of the pure lines and the  $F_1$ . From table 3 it can be seen that both the actual parent lines have a variance between 4 and 5 and the  $F_1$  is known to keep at about the same value. This makes it probable that the average variance of the genotypes segregating out of the cross will be about 4—5. Since there may appear types which are more easily modified than the parental types we might take 5 as the most probable value of the average variance caused by environment. This again allows us to remove part of our residual value of 3425. Thus:

	Sum of squares	Degrees of freedom
External and genic modifiers .....	3425	250
Environment ( $254 \times 5$ ) .....	1270	0
Residual = other genes than $X_a$ and $Le$	2155	250

Provided that we have got a reasonable estimate of the environmental variation we can say that the influence of genes other than  $X_a$  and

*Le* is of about the same size as *their* effects. No more strong genes have been traced and it is most probable that the residual genic variation is caused by what is called modifiers. This point of view is supported by the fact that it has been possible to select from this cross dwarfs, i. e. carrying one of the two late main genes, which flower 3 days earlier than the early parent line. The general experience from all the other crosses also points to the existence of a number of modifying genes.

#### SERIES OF MULTIPLE ALLELOMORPHS OR POLYMERIC GENES AS THE CAUSE OF QUANTITATIVE VARIATION.

SIRKS (1929), followed by others, considered it questionable whether the wide range of variation found in most quantitative characters could rightly be explained as the result of large numbers of small factors at work. He also emphasized the fact that in most cases the genetics of quantitative characters are not properly investigated but just assumed to belong in the kingdom of polymeric factors. In their place he wanted to set series of multiple allelomorphs combined with the assumption that the genes determining the quantitative characters show some special affection for mutating. Later SIRKS (1933) has adopted a somewhat different view on these questions, admitting the existence of several co-operating (polymeric) genes but keeping the door open to series of multiple allelomorphs. Since in the case of the flowering time of the pea two co-operating factors have been demonstrated and have been shown respectively to be linked to or identical with certain morphological factors there can be no question that at least a great part of the variation in flowering time in *Pisum* is caused by distinct and stable genes, thereby showing that multiple allelomorphs cannot be the only source of quantitative variation.

#### INTERACTION BETWEEN THE FLOWERING TIME GENES.

The *Le*—*le*-pair of genes is unusually well fitted for research in the field of quantitative inheritance because these factors have a quantitative effect and because they can be found wherever they occur, thanks to their morphological effects. As has been indicated in the introduction, the question of how quantity genes interfere with each other's phenotypical expression is of fundamental importance to our understanding of the hereditary phenomena.

In table 6 the crosses are arranged in the order of the average flowering time of the  $F_2$  and the difference between *Le*- and *le*-types

in  $F_2$  is given. Because the pure line crosses and the segregate crosses were worked in two years with so different weather conditions as 1926 and 1933 each of these series has been arranged in a special group.

TABLE 6. *Average flowering time and difference in flowering time Le-le-types of  $F_2$ .*

	Average flowering time of $F_2$	Diff. <i>Le-le</i> in $F_2$
St $\times$ Gd .....	+ 3,54	- 1,55
Gj $\times$ WW .....	+ 2,85	- 2,73
EsII $\times$ Buxb .....	- 0,24	- 3,68
Bism $\times$ Gd .....	- 0,58	- 1,50
Bism $\times$ Buxb .....	- 5,19	- 4,46
LRT II $\times$ St .....	+ 4,37	- 2,17
» $\times$ EsII .....	- 0,84	- 4,18
HRT II $\times$ Gd .....	- 3,48	- 1,85

Table 6 shows that there is, in general, a regression of the difference on the average: when the whole  $F_2$  is late the difference is small, and the more the average moves in the early direction the greater the difference becomes. Two of the crosses in which Gd partakes disturb the order, the first Gd-cross happening to fall into its proper place. This cannot, however, eradicate the general correlation between the two measures. We may thus conclude that in so far as the *le*-gene is dependent upon the general genic constitution of the individual carrying it and in such a way that, in general, a piling up of late genes (working in the *same* direction as *le*) diminishes the effect of *le*. The previously mentioned skewness of the  $F_2$ -distributions supports this result.

Finally, the dependency of *le* on the other genes can be demonstrated within the several  $F_2$ -populations. The comparison between *Le-* and *le*-types within respectively A- and a-group has been made in the four crosses where the number of individuals is great enough to allow of any accuracy in the comparison. The result is given in table 7 and shows that in every case the effect of *le* is lower in the A-group.

In questions like this, there is often considerable difficulty in bringing forward enough material to give firm statistical basis to the conclusions. Still, when a series of results from different angles bearing upon the same problem all point the same way it gives full biological significance and further may be brought into statistically satisfactory



shape with the expenditure of a certain amount of labour. The  $F_2$ -distributions are skew and that points towards an interaction between the factors for lateness, so much the more so, as the environmental modification curve is skew in the other direction. The effect of *le* in different crosses is clearly dependent upon the general lateness in the  $F_2$ -population (table 6). This is just what should be expected on the basis of the interaction hypothesis. Within the several  $F_2$ -populations the effect of *le* is lower in the late group (A) than in the early group (a). (Table 7.) All these facts brought together give a very good demonstration of the interaction between quantity genes on the general lines of the interaction hypothesis. The demonstration of the existence of such a phenomenon definitely puts the interaction hypothesis into the category of a theory.

TABLE 7. *Difference Le-types—le-types in A- and a-groups of different crosses.*

	Difference in flowering time of <i>Le</i> — <i>le</i>	
	A-group	a-group
Gj × WW .....	— 2,61	— 3,45
Gd × St .....	— 1,85	— 2,03
Bism × Gd.....	— 1,64	— 2,36
LRT II × St .....	— 0,98	— 5,00

Further investigations in quantity genetics lead via the interaction theory into the wide field of the relations between gene, cytoplasm, environment and phaenotype, since different assumptions concerning these relations lead to different consequences as to the reaction curve of the individual. The time seems already now to have come where we can plan useful co-operation between genetical and physiological research (for instance: concerning the physiological reaction in flowering time of different genotypes). Such research may be expected to add considerably to our knowledge of the fundamentals of heredity.

The interaction between the quantity genes may also make it possible to use them for experimental tests of FISHER's theory on evolution of dominance.

## SUMMARY.

This paper on flowering time in peas is the first in a series of reports under preparation concerning investigations in quantitative genetics in peas.

A short review of the results obtained by previous workers on the genetics of flowering time in *Pisum* is given, showing that still considerable confusion prevails concerning this question.

It is demonstrated that two main factors, both showing partial dominance towards lateness, are at work in the material investigated. They seem to be responsible for about half the genic variation within the  $F_2$ -populations. The other half of the genic variation is probably due to modifiers.

One of the main genes is linked to the A-gene for flower colour, and the other is either the *le*-gene (internode length) itself or closely linked to it.

The flowering time genes are demonstrated to interact in the manner to be expected from the author's interaction theory.

The results presented demonstrate a case where a quantitative character clearly is governed by distinct co-operating genes and contradict SIRKS' hypothesis for quantitative inheritance.

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# AMPHIPOLYPLOIDY IN THE HYBRID *FESTUCA ARUNDINACEA* × *GIGANTEA*

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## INTRODUCTION.

THE cross-pollinating grasses furnish many examples of species hybridisation. Although many species hybrids have been found to be naturally occurring, only a small number of all possible combinations are described as spontaneous hybrids. From experimental investigations new examples of interspecific and intergeneric hybrids in grasses are delivered. The present writer has successfully crossed the species *Lolium multiflorum* and *Festuca gigantea* (F. NILSSON 1930 a) and JENKIN (1924, 1933) has contributed many different combinations. In most cases the experimental results agree with the taxonomical statements in morphological characters but the sterility phenomenon cannot be clarified only by taxonomical studies. In several cases an interspecific hybrid in taxonomical publications is said to be quite sterile, but a close investigation of experimental material has shown that the sterility is very often incomplete or absent. References are made to *Lolium multiflorum* × *L. perenne* (F. NILSSON 1930 b, JENKIN 1931), *Bromus hordeaceus* × *B. mollis* (F. NILSSON 1931) etc. In other cases progeny of primary hybrids can be obtained but by back-crosses (F. NILSSON 1933, JENKIN 1933, JENKIN and SETHI 1932).

In this paper some results will be given from an investigation of the interspecific hybrid *Festuca arundinacea* SCHREB. × *F. gigantea* VILL. Statements as to natural hybridisation between these two species are very few. HOLMBERG (1926) reports the hybrid from three localities in Sweden and ANDERSEN (1931) states that the hybrid is found in two localities in Denmark. From other countries reference can only be made to SAINT-YVES (1929). From experimental research some results are published by JENKIN (1933), who successfully crossed the two species in both directions in 1930. Cytological observations in the same material were made by PETO (1933).

## MATERIAL AND METHODS.

The material for the present investigation consists of natural hybrids partly from hybridisation in nature and partly from spontaneous

crosses in breeding material. One individual was obtained in 1928 from the Botanical Garden at Lund, to where it was transplanted from its locality in South Sweden. A clonal cutting was planted at Weibullsholm, where the author was stationed at that time. That plant was vegetatively propagated on a big scale in order to get a possibility of making closer investigations with regard to modificatory variation and fertility.

The other part of the hybrids, consisting of 8 individuals, appeared in the grass material in 1930. One plant of *Festuca arundinacea*, No. 5357, was harvested after open pollination in 1929, and among 100 spaced seedlings 8 individuals showed themselves not to be pure *F. arundinacea*. They were observed already in 1930, and in 1931 they were found to be products of hybridisation with *Festuca gigantea*. The mother plant had been surrounded firstly by *F. arundinacea* and secondly by several other species, among which *F. gigantea* was also represented.

Direct crossing experiments, on a small scale, between the mentioned species were performed in 1928 in order to get a control for the transplanted spontaneous hybrid individual. The result was however negative, no heavy seed being obtained, which may be due to unfavourable conditions, because JENKIN (1933) met with good success in his crosses.

The investigation of male fertility was made by determining the development of the pollen at the time for the anthers' dehiscence. At least three counts were made of the number of normally appearing pollen grains with nuclear and cytoplasmic contents. The anthers were taken from different florets in the inflorescences.

The seed-setting was determined by counting the number of developed seeds. For this purpose a diaphanoscope has been used. In 1933 the weight of 100 florets was determined and after that the floret number for the whole plant was easily calculated.

The somatic chromosome numbers were stated in slides of root tips fixed in NAVASHIN's fixative and stained in HEIDENHAIN's iron-haematoxylin. In 1933 gentian violet was also used.

The meiotic studies were made in pollen mother cell material and fixation was made with FLEMMING's solution. The slides were stained with gentian violet. Before fixation the proper stage of development was determined by BELLING's aceto-carmin method. The sections were cut to 16  $\mu$  and the figures were drawn with the aid of a LEITZ drawing camera.

For valuable assistance in the work I am indebted to Mr. E. ÅBERG, Uppsala, and my wife, Mrs. MARTHA NILSSON.

## RESULTS.

### MORPHOLOGY AND FERTILITY.

In the literature I have not found any complete description of the hybrid between *Festuca arundinacea* and *F. gigantea*. It is said by HOLMBERG (1926) to be sterile and difficult to distinguish from the hybrid *F. gigantea*  $\times$  *F. pratensis*. »It is however coarser with lighter sheathes, stiffer leaves and the spikelets are richer in florets.»

The individuals investigated by the present writer did not differ in any essential character. The transplanted individual is, however, more prostrate and less tall than the others, which are very uniform in type.

The hybrid is intermediate between the parental species in most characters, but the awn character from *F. gigantea* is almost completely dominant. To the essential characters the following description may be given. A coarse tussock with



Fig. 1. a: *Festuca arundinacea*, No. 5357, b: *Festuca arundinacea*  $\times$  *F. gigantea*, No. 338, c: *F. gigantea*, No. 320.

prostrate growing straws, which reach a length of 115—125 cm. Straws and sheathes are scabrous. The leaves are 6—10 mm broad, terminating in a slender point. Extended big auricles. The panicle is rather thin, partly one-sided with scabrous panicle branches. The glumes are pointedly deltoid, winged, the lower one triple-nerved, the upper one five-nerved. Outer palea with five indistinct nerves, slightly

rough, its upper margins membranous, 6—10 mm long with a 3—4 mm awn. The spikelets are 8—12-flowered. The hybrid comes into flower nearly as early as *F. arundinacea*, i. e. about a week earlier than *F. gigantea*. It continues to produce inflorescences and flowers during the whole summer.

The pollen development of the transplanted individual, No. 338, has been investigated every year from 1929 to 1934. Under the microscope the pollen is generally seen to be degenerated and empty. In 1932 many different anthers were investigated and a very few pollen grains were found to be filled with cytoplasmic contents. The same results were obtained in the years 1933 and 1934. In exceptional cases it seems, therefore, as if normal pollen grains could be produced. If these normally appearing pollen grains, of which only a couple or two were noticed in a spikelet, are also functional is a question of great importance, but it cannot be answered with certainty at present. Even if they are functional they are not likely to be able to fertilise, because the anthers have not been seen to dehisce but are at that time often shrivelled. The seedling plants, No. 1080, arisen in 1930, have been investigated in pollen development in the years 1931—1934, but no normal pollen grains have as yet been seen. The mother plant of *Festuca arundinacea* was found in 1930 to give 97 % normal pollen grains.

In the year 1930 attempts were made to back-cross the  $F_1$ -plant No. 338 with the parental species. Without emasculation pollinations were made on a big scale, partly with *F. arundinacea* and partly with *F. gigantea*. The result was negative, no heavy seed being obtained.

In trying to get some progeny of the  $F_1$  hybrid nearly all the panicles have been allowed to open pollination every year. When the hybrid plants have been surrounded by several plants of the parental species sufficient pollen may have been delivered for fertilisation. In 1929 no seed was obtained but in 1930 four heavy seeds were harvested from a lot of panicles on seven plantlets of No. 338. Of these seeds two showed power of germination and gave rise to established plants. In the year 1932 only 27 panicles developed, because of transplanting the material. In the following year, 1933, the plants showed a rich development of panicles again. No seed was obtained, although about 162,000 florets were harvested and investigated on seed-setting. From the hybrid plants No. 1080 no seed has hitherto been found. These individuals, however, have not been vegetatively propagated on the same scale as No. 338.

From the fertility tests made during the years 1929—1933 only two progeny individuals have been raised. It may therefore be concluded that the hybrid is very highly sterile, not only male sterile but also female sterile. Only in exceptional cases are viable gametes produced capable of fertilising.

#### HYBRID DERIVATIVES.

The raised progeny individuals, No. 1866/3 and No. 1866/5, differ very much from each other. Both of them are coarse, robust and more erect than the  $F_1$  hybrid.

The former does not appear in any way to descend from a hybrid between *F. arundinacea* and *F. gigantea*. (Cp. fig. 2.) It reaches a height of about 1.5 m. The straws and leaf sheathes are nearly glabrous, the leaves are 13—18 mm broad, acuminate, with small auricles. The panicle is very peculiar, having very short primary panicle branches, the spikelets being agglomerated at different heights. The glumes are pointed and winged, the lower one one-nerved, the upper one triple-nerved. The outer palea is narrowly winged, rather distinctly nerved, the dorsal nerve finely serrated, awnless. From the morphological characters it appears to be more of a hybrid between *F. arundinacea* and *F. pratensis* than a derivative of the hybrid *F. arundinacea*  $\times$  *F. gigantea*. Its fertility was investigated during the years 1932—1934. The pollen grains are generally degenerated and empty but single grains appear to be indecisively filled with contents. The same observations were made in all the years. It has not been possible to decide whether any of the pollen grains are viable and functional. No seed could be harvested, although about 17,000 florets were openly pollinated and investigated on seed-setting in 1933. Up to the present the plant has been found to be quite sterile.

The other progeny plant, No. 1866/5, resembles the mother plant very much but is taller and more robust (fig. 3). It is about 1.5 m high, erect and very coarse. The leaf sheathes and straws are scabrous, the leaves 15—20 mm broad. The panicle is large and spreading, with large spikelets, big paleas and long awns. The fertility is surprisingly high compared with that of the  $F_1$  hybrid and the progeny plant mentioned before. The pollen development was investigated during the last three years and the percentage of normally appearing pollen grains was found to be 53.9 and 55.8 in 1932 and 1933 respectively. In 1934 it was still higher and seemed to be quite normal, with an average of 91.2 %. In 1932 isolation tests were made but no seed were



set. Only few panicles were left for open pollination and the seed-setting was nil. In 1933 all the panicles were openly pollinated and 30 heavy seeds were harvested from about 19,000 florets, which gives a percentage of seed-setting of 0,16. This individual thus gives a very



Fig. 2. No. 1866/3, a derivative of the hybrid *F. arundinacea*  $\times$  *F. gigantea*.  $2n = 28$ .

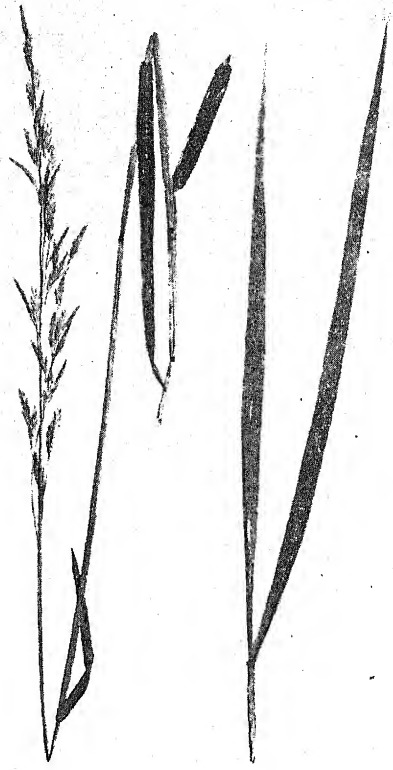


Fig. 3. No. 1866/5, an amphipolyploid derivative of the hybrid *F. arundinacea*  $\times$  *F. gigantea*.  $2n = 84$ .

low degree of seed-setting in spite of the fact that the pollen development appears to be good.

The harvested seeds were put to germination in the summer 1934. The power of germination is rather interesting, because some of the seeds germinated very quickly while others need at least 4 months to develop seedlings. Consequently, the germination energy is very low and some of the seedlings were somewhat weak and died at an

early stage of development. At present 17 seeds have germinated and 8 seedlings are developing rather well. Three of them have really passed the seedling stage.

#### CYTOLOGICAL OBSERVATIONS.

The somatic chromosome number in the species *F. arundinacea* has been determined by several authors. EVANS (1926) found about 40 chromosomes in root tips and gave the haploid number as 21. The somatic number 42 was found by LEVITSKY and KUZMINA (1927), STÄHLIN (1929) and RADELOFF (1930). PETO (1933) states that one plant of *F. arundinacea* »contained a small chromosome or fragment in addition to the normal number of chromosomes». The somatic complement of *F. gigantea* is also found to be 42 (STÄHLIN, PETO). In the present investigation several different types of *F. arundinacea* were fixed and in all of them the number of somatic chromosomes was determined at 42. Of *F. gigantea* only one type was investigated. The result agrees with those of the above-mentioned authors.

The somatic numbers of the hybrid plants were counted in root tips and all the described plants showed the number 42 (fig. 4), which was to be expected from the morphological determination of the hybrids.

Meiotic studies were made by PETO (1933), who published data on the meiotic behaviour in the  $F_1$  hybrid. In the heterotypic metaphase PETO found univalents and bivalents as well as trivalents and quadrivalents. On an average 14 univalents were found, of which PETO writes: »This indicates that there is a fairly constant failure of pairing between seven chromosomes from each parent».

In the present investigation of  $F_1$  the plant numbers 338 and 1080 VI/1 have been studied as regards meiotic behaviour. The observations made are mostly in agreement of those of PETO. The highest number of univalents found is 14 but very often it is lower. The univalents lag behind in the metaphase plate after the bivalents and poly-

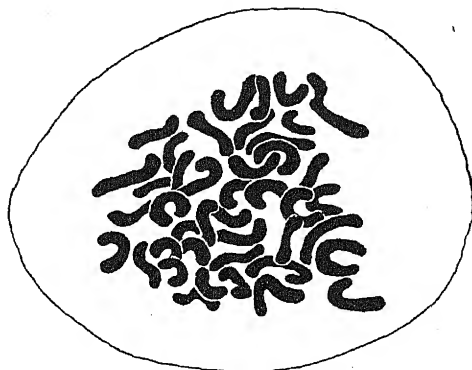
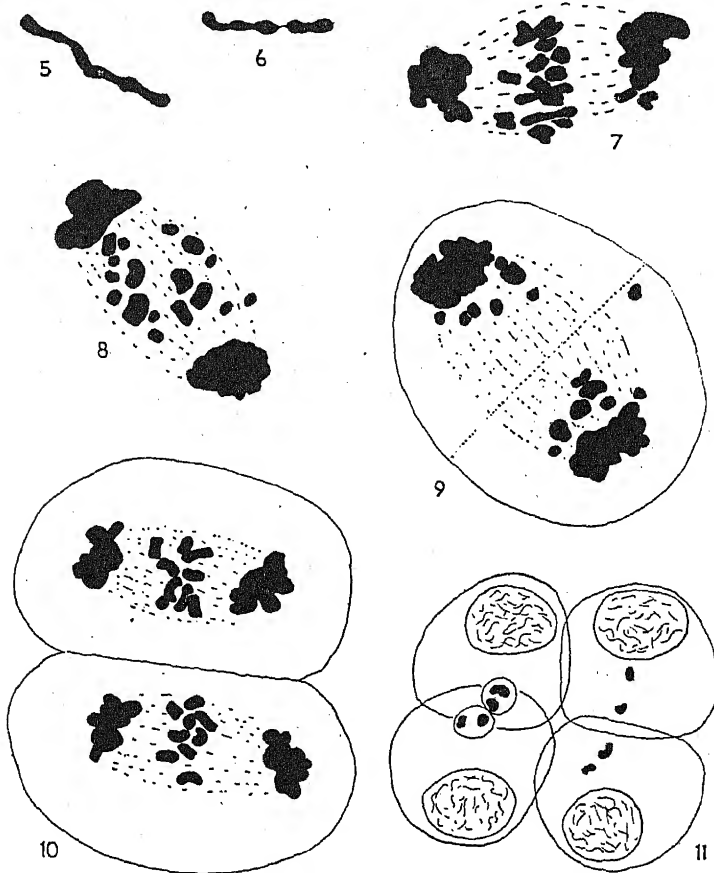


Fig. 4. Somatic metaphase plate of the  $F_1$  hybrid *F. arundinacea*  $\times$  *F. gigantea*.  
 $2n = 42$ . (Magn. 1800  $\times$ .)

valents have separated to the poles. One quadrivalent is seen in many pollen mother cells and also trivalents have been seen, but not in any definite number (figs. 5 and 6). Some of the univalents divide equationally, in agreement with PETO's observations, but it does not seem to be the case with all of them. In fig. 7 are seen 14 univalents,

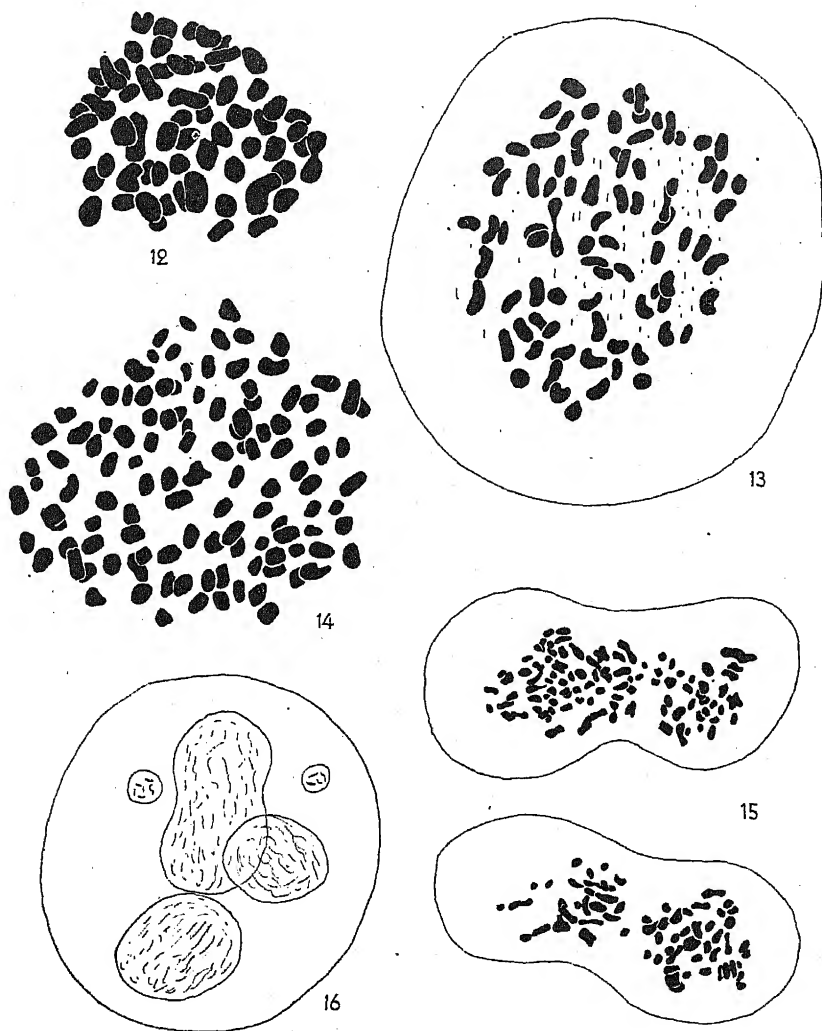


Figs. 5—11. Meiotic divisions of the  $F_1$  hybrid, plant No. 338. — Figs. 5 and 6. Quadrivalent and trivalent. — Figs. 7 and 8. Heterotypic anaphase plates. — Fig. 9. Heterotypic telophase with splitted univalents. — Fig. 10. Homeotypic anaphases. — Fig. 11. Tetrad with microcytes and single chromosomes.  
(Magn. 1800  $\times$ .)

two of which certainly divide. Fig. 8 also shows 14 univalents, 5 of which are divided and 7 undivided. As a rule they reach the poles in time to get included in the daughter nuclei but that is not always the case (fig. 9). Probably it is a common occurrence for some univalents to divide in the heterotypic metaphase while others go un-

divided to the poles. This has also been noticed in the hybrid *Triticum dicoccum*  $\times$  *T. monococcum*.

In the homeotypic division the univalents also lag behind, the undivided ones split and the others segregate at random (fig. 10). After



Figs. 12—16. Meiotic divisions in the  $F_1$  hybrid plant No. 1080 VI/1. — Fig. 12. Heterotypic metaphase plate with doubled chromosome number. — Fig. 13. Homeotypic anaphase with 42 chromosomes to each pole. — Fig. 14. Heterotypic metaphase plate, polar view. — Fig. 15. Syndiploid heterotypic metaphase, two sections. — Fig. 16. Semiheterotypic and heterotypic divisions in the same P.M.C. (Magn. 1800  $\times$  except fig. 15 with 700  $\times$ .)

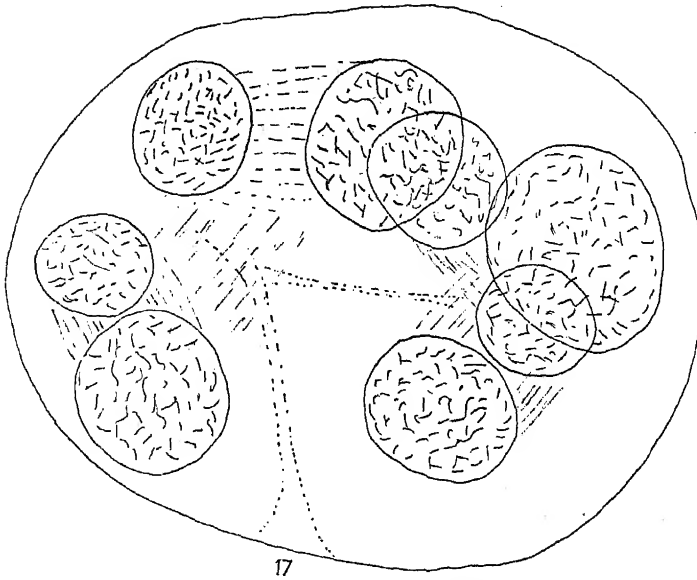
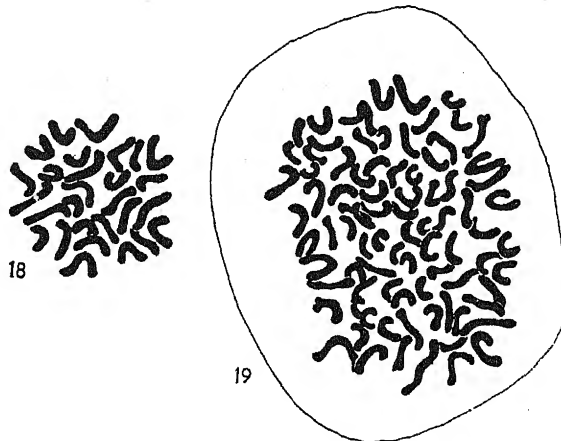


Fig. 17. Multinucleate P. M. C. (Magn. 1800  $\times$ .)

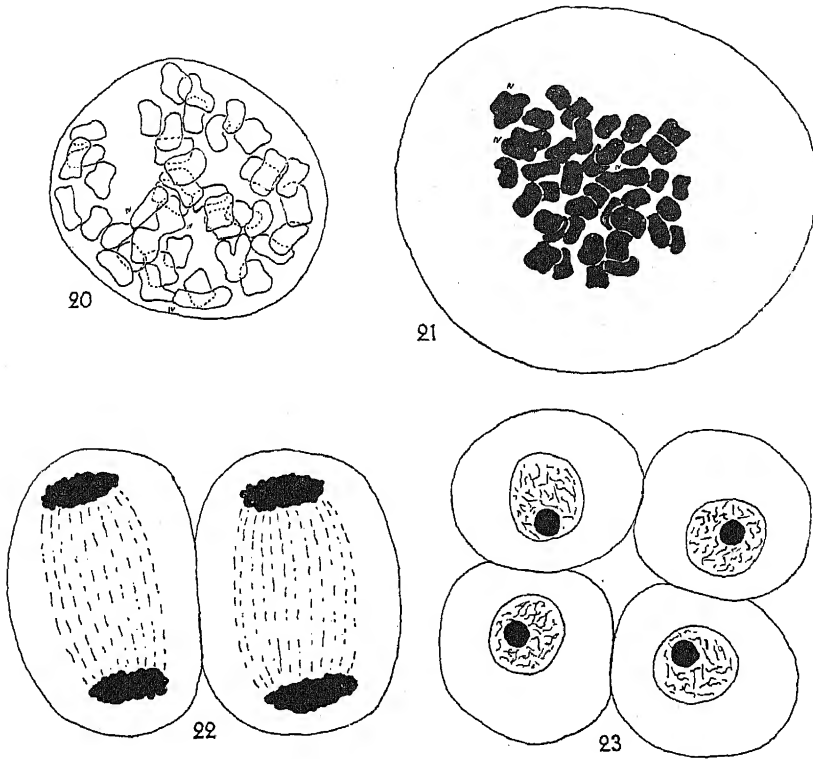
the homeotypic division is finished the development generally ceases and degeneration occurs. Several cases of developed tetrads, however,



Figs. 18 and 19. Somatic metaphase plates of the hybrid derivatives Nos. 1866/3 and 1866/5.  $2n = 28$  and  $84$  respectively. (Magn. 1800  $\times$ .)

have been observed where wall formation has taken place. In fig. 11 a tetrad is shown with microcytes and single chromosomes lying in the plasma.

No case of polyploid microspores has as yet been noticed in the plant number 338. In the other investigated  $F_1$ -plant, No. 1080 VI/1, polyploid and multinucleate pollen mother cells were quite frequently seen. Fig. 12 shows a heterotypic metaphase plate with 62 units of bivalents and quadrivalents and in fig. 13 is seen a homeotypic anaphase after failing of the reduction division. The result will be a



Figs. 20—23. Meiotic divisions of the amphipolyploid plant No. 1866/5. — Fig. 20. Diakinesis stage. — Fig. 21. Heterotypic metaphase plate. Polar view. — Fig. 22. Homeotypic telophases. — Fig. 23. Normal tetrad. (Magn. 1800  $\times$ .)

dyad instead of a tetrad. A very high number is shown in fig. 14, where 116 units of smaller and greater magnitude are counted. The high number may be considered to have arisen from doubling two times. Another example is given in fig. 15, where a fusion is clearly seen between two daughter nuclei. The last-mentioned case is a syndiploid metaphase in which the two metaphase plates already reached the double number through one doubling before the meiotic

divisions. Through a combination of doubling before and during the meiotic divisions the high numbers are clearly understood. Failure of wall formation between daughter nuclei seems to be the cause of most of the high chromosome numbers. In single anthers failure of wall formation is commonly seen at different stages. In fig. 16 a fusion between two daughter nuclei takes place at the same time as another division is just finishing in the same cell. Wall formation has not occurred and two micronuclei are seen. When the wall formation fails, even before the meiotic divisions, giant multinucleate pollen grains arise, which was noticed in a couple of anthers (fig. 17).

The progeny plants, Nos. 1866/3 and 1866/5, differ in the chromosome complement, as was to be expected from the morphological characters. The former has the somatic number 28, while the latter reaches the number 84 (figs. 18 and 19). No. 1866/3 has not been studied to such an extent that definite results can be published with regard to meiotic behaviour. No. 1866/5 is more intensively studied in meiosis. The heterotypic division seems to be quite regular and no univalents are seen. All the chromosomes show conjugation and besides bivalents also quadrivalents are found to a number of at least three (fig. 20). Also at the metaphase stage three quadrivalents have been observed (fig. 21). The homeotypic division is found to be regular and after the homeotypic divisions, as a rule, normal tetrads are developed, which give rise to a high percentage of normal pollen grains (figs. 22 and 23). The normal reduction division is in good agreement with the stated good pollen development and it is quite clear that a fertile derivative of the hybrid *Festuca arundinacea*  $\times$  *F. gigantea* has arisen, which obtained its fertility through chromosome doubling. From hybridisation between the parent species, each with  $n = 21$  chromosomes, is built up a new type containing  $n = 42$ , i. e. a summation of the parents' complements.

## DISCUSSION.

From the results of the present investigation it may be concluded that the species *Festuca arundinacea* and *F. gigantea* easily hybridise with each other when they are grown together. In one case 8 % spontaneous hybrids were found in the offspring of one plant of *F. arundinacea* surrounded by *F. gigantea*. As already pointed out by JENKIN (1933) natural hybrids have not been found so often and the

reason can only be the distinctly different habitats which do not give many opportunities for spontaneous crossing in nature.

The cytological observations agree with those of PETO (1933) and may admit the conclusion being drawn that the parent species, at least to some extent, have the same phylogenetic origin. The pairing between chromosomes from each parent indicates homology between chromosomes in the different species, and the polyvalent associations homology between chromosomes within the species genomes. When the basic number in the genus *Festuca* is 7 and the mentioned species both have the number 21 they may be regarded as polyploids and as such descendants from diploids and tetraploids. Moreover it seems probable that both the species are built up as allo-polyploids and one genome of 21 chromosomes contains three 7-genomes, one of which at least has the same origin in both the species. Through inter-crossings between each of the parent species with a third species, i. e. *F. pratensis*, it is really found that the hybrids from these crosses cytologically behave on the whole in the same manner. These inter-crossings are easily made (JENKIN 1933, and unpublished results by the present writer) and the hybrids occur naturally. Both of them are capable of chromosome conjugation. Indeed at least seven bivalents are found in each of them and therefore it seems possible to conclude that a close relation exists between the three species. JENKIN (1933) discussed the problem from the view of his compatibility tests and reached the same conclusion as regards the species *F. arundinacea* and *F. gigantea*: »The ease with which they can be inter-crossed with *F. pratensis* suggests that this species (or its progenitor) has in some degree at least entered into both polyploids . . .». That suggestion is supported by the cytological observations (unpublished results) and by the behaviour of progeny plant No. 1866/3 (comp. below).

From the offspring of the  $F_1$  hybrid *F. arundinacea*  $\times$  *F. gigantea* it is clear that this hybrid is in some way capable of producing viable and functional gametes. The one progeny plant has a reduced chromatin mass in relation to the mother plant, having the somatic number 28 instead of 42. This reduction may only be possible in two ways: 1) by inter-crossing with a third species with a low chromosome number, and 2) by reduction in the zygote after fertilisation. From the meiotic studies it is found that the probably functional gametes may have the chromosome number about 21 or the unreduced number 42 or a multiplication of 42. The possibility of back-crossing with one of the parents should result in an offspring with at least 42 chromo-



somes and 14 chromosomes should have to be ejected. It does not seem probable because in that case a reduced nucleus would probably be balanced and give rise to a fertile individual. It therefore seems more probable that a female gamete with the number 21 has been viable and fertilised by a *F. pratensis* gamete with 7 chromosomes. Most of the hybrid 21-gametes are of course not viable, but in exceptional cases it must happen that these 21 chromosomes belong only to *F. arundinacea* or to *F. gigantea* and may be supposed to be viable. If the female gamete with 21 chromosomes which is supposed to be fertilised by a 7-gamete from *F. pratensis*, contains only or nearly only chromosomes from *F. arundinacea* it is easily explained why the product does not resemble the species *F. gigantea* very much but more the species *F. arundinacea* and *F. pratensis* (comp. above). If the plant No. 1866/3 really is a product of crossing between  $F_1$  and *F. pratensis* it strongly supports the suggestion of a near relationship between the three species.

The progeny plant No. 1866/5 is no doubt a product of chromosome multiplication in some way. Unreduced gametes may be as common in the female as in the male organs and it may be presumed that all the unreduced gametes are functional in fertilising if they get opportunities to do so. If two unreduced gametes have the possibility of meeting each other the result will of course be a zygote with a multiplied chromosome number. Although the anthers as a rule are non-dehiscent the possibility of single unobserved dehiscing anthers must not be excluded. In that case the progeny would simply be the product of self-fertilisation, analogous to the *Phleum*-case (GREGOR and SANSOME 1930). The other possibilities of a doubling from 42 to 84 seem only to be an apogamous development of female gametes with an unreduced or multiplied chromosome number, in the first case accompanied by a doubling in the zygote. Apogamous development of female gametes is assumed by LEVITSKY and BENETZKAJA (1930) and by LEBEDEFF (1934) to have caused the amphidiploid plants in the wheat-rye hybrids. In these cases the amphidiploids occurred more frequently and no real objection can be raised to the assumption of apogamy. In the *Festuca* hybrid, however, only one single amphipolyploid has arisen in the course of 5 years and therefore an assumption of apogamous development is very improbable, but if apogamy is the way of producing the amphipolyploid type it seems most probable that the female gamete had the multiplied number 84 already before developing into a zygote. Even in that way we must suppose a more

frequent occurrence of polyploid types and so it must be more plausible to assume a sexual way of propagation. We may also assume that a reduced female gamete with the chromosome number 21 is fertilised by a male gamete of one of the parent species accompanied by a somatic doubling in the zygote. Judging from the morphological characters, however, it does not seem to be the way, because the new polyploid type is intermediate between the parents and quite similar to the  $F_1$  plant.

The pollen development of the new polyploid plant with the somatic number 84 is really not normal as might have been expected from the cytological behaviour with normal reduction division. It is worth noting that the percentage of normal pollen grains during the first two years is given at slightly more than 50 but the third year more than 90. Due to different causes the fertility in new allo-polyploids is generally found to be somewhat low in the first generation. Very common meiotic irregularities are responsible for the lowered fertility. In the amphidiploid *Crepis rubra*  $\times$  *foetida* (POOLE 1931) the percentage of good pollen was found to be only 35, probably caused by multivalent associations. *Galeopsis*, *Aegilotricum*, *Nicotiana* and *Saxifraga* also showed a relatively low degree of fertility in the first generation. In later generations a stabilisation occurs and fully fertile lines are obtained. In the allo-polyploid plant of *F. arundinacea*  $\times$  *F. gigantea* multivalent associations are observed and although detailed studies in that respect hitherto fail it is not without reason to suspect a somewhat disturbed segregation in the heterotypic division, which may be one of the causes of the lowered fertility. The different percentages in different years give reason to think that the relation between viable and unviable gametes may be altered to a great extent through modifications. Further studies are necessary to clarify the fertility results.

The low seed-setting capacity is another question which must be kept apart from the gamete development, provided that this is sufficient for fertilisation and seed-setting. When only one single individual exists with the amphipolyploid number 84 no cross-pollination is possible without hybridisation. Therefore one has to judge the possibilities of self-fertilisation and hybridisation with the parent species. As regards self-fertility one of the parents, i. e. *F. arundinacea*, shows a low capacity, but it is rather high in *F. gigantea* (BEDDOWS 1931). LAWRENCE (1930) pointed out that the degree of self-sterility is different in diploids and polyploids, and MÜNTZING (1932) discussed the same

thing in connexion with the *Galeopsis*-case. According to LAWRENCE the self-sterility mechanism may be disturbed by chromosome doubling. As a rule the self-fertility is greater in polyploids than in diploids. (Comp. also F. NILSSON 1934). As the parents in this case must already be regarded as polyploids the new polyploid need not necessarily show any difference in self-fertility from the parents. Anyhow there does not seem to be any increase in the degree of self-fertility when seed-setting only was observed in one year at 0,16 %.

From other polyploid series it is known that new types with a multiplied chromosome number can only with difficulty be back-crossed with the parental species, e. g. *Raphanobrassica* (KARPECHENKO 1928), *Primula kewensis* (NEWTON and PELLEW 1929), *Galeopsis* (MÜNTZING 1932). Obviously the same difficulty is met with in the *Festuca*-case, because the allo-polyploid plant was surrounded by both *F. arundinacea* and *F. gigantea* without any great seed-setting. Consequently the offspring must be regarded mainly as results of self-fertilisation, which may however be easily judged from investigations of the progeny plants.

### SUMMARY.

From the hybrid *Festuca arundinacea*  $\times$  *F. gigantea*, which is highly sterile, two progeny plants were obtained after open pollination. The  $F_1$  hybrid is found to have the somatic chromosome number 42 as the parent species, but the progeny plants differ very much from each other, one having the somatic number 28 and the other 84. The former is explained to have originated by inter-crossing between  $F_1$  and a third species *F. pratensis*, which agrees with the morphological characters, the latter is a new instance of chromosome doubling after species crossing, giving a new polyploid type intermediate between the parents and highly fertile in comparison with  $F_1$ .

The new intermediate amphipolyploid plant is found to have slightly more than 50 % normal pollen grains in two years but the third year more than 91 % was observed. The seed-setting capacity is low on account of self-sterility and difficulty in back-crossing with the parents. In several respects the new polyploid type seems to establish a new species, having summed up the chromosome complements of the parents and being intermediate in morphological characters.

Undrom, Sept. 1934.

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# IS THE SHAPE OF THE LACTATION CURVE GENETICALLY DETERMINED?

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CATTLE breeders and agricultural researchers who have made dairy cattle a special object of study and for this purpose generally draw up diagrams of the different lactation curves cannot have avoided noticing that the *shape* of the curves for the different lactation years — or more correctly the rate of decline of the curves — for the individual animals shows in the main very great similarities, but considerable differences are at once apparent when the lactation curves of different animals are compared with each other. If positive evidence could be advanced that this is really the case it would then imply that the shape of the curve is determined by the constitution of the cow, and in that case it seems very probable that the shape of the lactation curve is an inherited character. This conception has also been advanced already by various investigators, who arrived at their conclusions from the study of different facts (SANDERS 1923, TURNER 1927, BRUN 1928, BECKER and MC GILLIARD 1928. See also summarized account given in the chapter on »Persistency», p. 25, by BUCHANAN SMITH and ROBISON 1933). The purpose of the present paper is not to attempt to furnish any positive proof of the hereditary or constitutional determination of the shape of the lactation curve, the material available is not extensive enough and adequate methods are wanting to acquire such proof. My intention is only to present a few very simple facts which appear to lend support to the view that hereditary factors play an important rôle in determining the shape of the lactation curve.

Very careful observations are made of the cows kept under the control of the Animal Breeding Institute. Among other things, the milk from each cow is weighed separately after each milking and samples for fat analysis are also taken from each milking. These samples are collected and kept for 3 or 4 days and analyses of fat content are therefore made twice a week. By the aid of these observations it is possible to plot lactation curves for the various cows which thus in fact correspond as exact as possible to the curves actually produced by the animals. All examples given in this paper are taken from material kept or controlled by the Animal Breeding Institute.

In Figs. 1 to 10 are shown all the lactation curves for 10 different cows drawn in accordance with the carefully kept records as described above. These curves do not however give the actual milk yield but the quantity of the so-called Fat Corrigated Milk (F. C. M.). (No great difference is obtained if the actual quantity of milk produced is drawn in the diagram instead.) The mutual correspondence between the different curves of the individual cows is so apparent that there is hardly any need of calling any particular attention to it. Of course it would be possible to select cows which do not show such a close agreement, but the agreement appears to be sufficiently common — and a still greater number of instances might be adduced if necessary — to warrant our regarding it as a matter particularly worth while observing and investigating. Now if we assume that this view is correct, that is, that the shape of the lactation curve is constitutionally determined, then it follows that we cannot obtain sufficient or complete knowledge of the individual cows by only giving their lactation yields without also giving the shape of their lactation curves. For instance, the cow Tita 458 (Fig. 1) produced 4493 kilos of fat corrigated milk during her first lactation year and the cow Egga 430 yielded 4369 kilos of fat corrigated milk during her second lactation year. Thus, the quantity of milk produced by these two cows during these lactation years was fairly equal. But it is obvious that the physiological processes underlying the production of milk during these two different lactation years must to a certain extent have been of a different nature, for otherwise the curves would have shown a greater similarity. The figure 4493 kilos or the calculated daily average yield (or this average as compared with the average in the herd) does not therefore seem to be an adequate description of the milking capacity of the first cow.

The impression that the shape of the lactation curve is constitutionally determined is supported to a certain extent by the results obtained from a few minor tests carried out at the Animal Breeding Institute. During the winter time when the cows are housed in cowsheds they are fed individually, all the different feeding stuffs being weighed for each individual cow. The food ration for each cow is calculated for each separate week, and this calculation is made on the basis of the quantity of milk produced during the preceding week (and also based on the animal's weight during the preceding week). In this way the cow is always given a quantity of feed equivalent to the requirement for the production of a definite quantity of

milk and — unless special feeding experiments are being carried on — this feed ration will as near as possible be suited to the quantity of

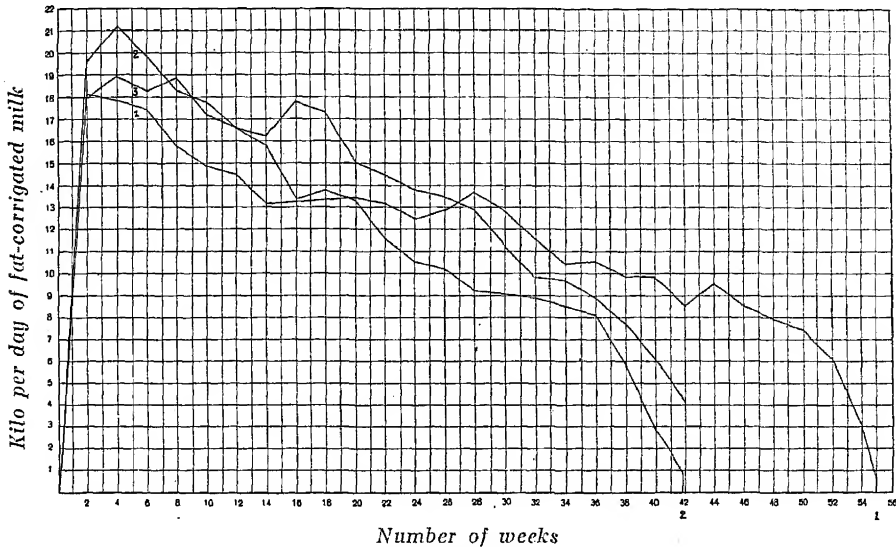


Fig. 1. Curves for the lactation years Nos. 1, 2 and 3 for the cow 458 Tita.

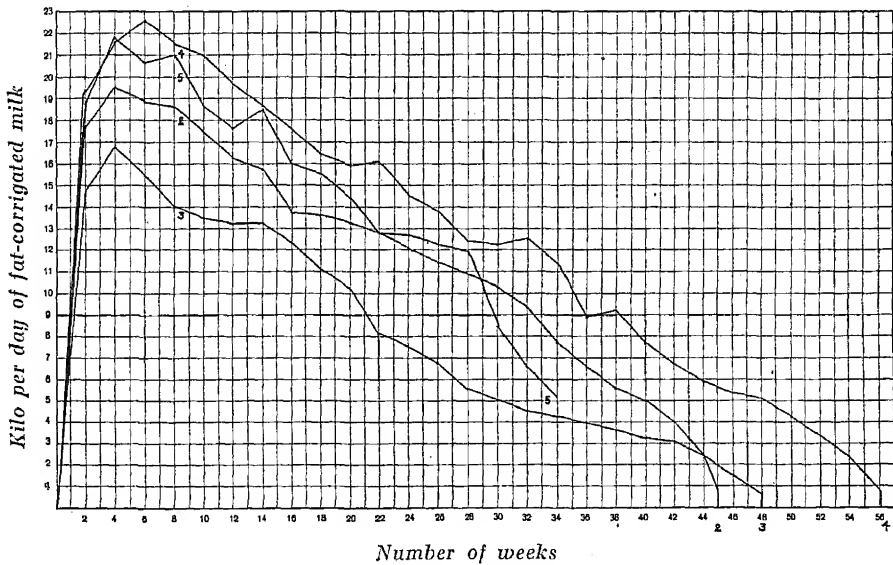


Fig. 2. Curves for the lactation years Nos. 2, 3, 4 and 5 for the cow 740 Idun.

milk actually produced by the cow. But in connection with certain overfeeding experiments (BONNIER and BÄCKSTRÖM 1935) two cows



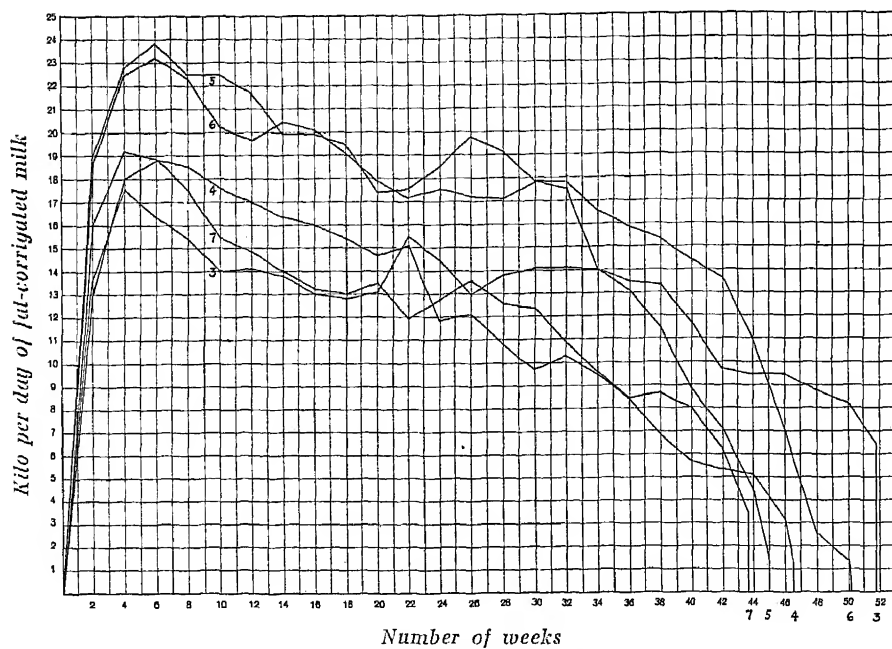


Fig. 3. Curves for the lactation years Nos. 3, 4, 5, 6 and 7 for the cow 414 Dutty.

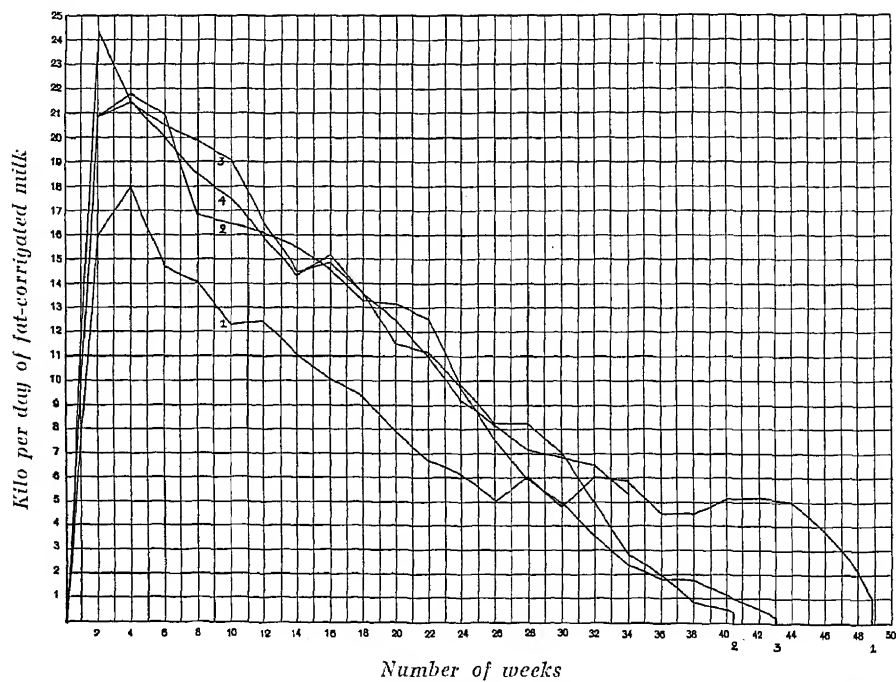


Fig. 4. Curves for the lactation years Nos. 1, 2, 3 and 4 for the cow 437 Åsa.

were selected which had shown a very rapid decline in their lactation curves during the preceding year. The overfeeding experiments with these two animals were carried on in such a manner that from a certain day and for a number of weeks following they were fed on a quantity of feed corresponding to a constant quantity of fat corrigated milk. For one of the cows (Kersti 707, Fig. 11) the experiment was started during her third lactation year, 4 weeks after the birth of the calf,

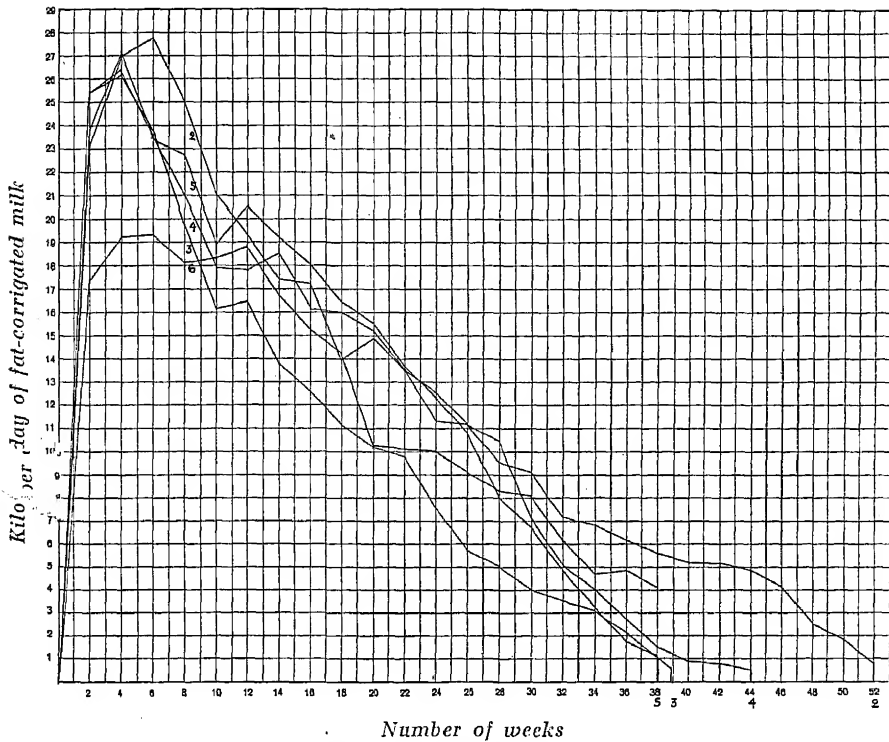


Fig. 5. Curves for the lactation years Nos. 2, 3, 4, 5 and 6 for the cow 430 Egga.

when she had attained her maximal milk yield, which amounted to a little more than 24 kilos of fat corrigated milk per day. From that day and for the following 10 weeks the cow was fed on a quantity of feed equivalent to 27 kilos of fat corrigated milk per day. The experiment with the other animal (Åsa 437, Fig. 12) was begun in her fourth lactation year, 8 weeks after the birth of the calf, when she produced a daily yield of a little more than 18 kilos of fat corrigated milk. From that day and for the following 12 weeks she was given a feed ration equivalent to 19 kilos of fat corrigated milk per day. But as appears

from the figures the lactation curve declined in both cases in a manner typical for the two animals in spite of this high degree of overfeeding.

These two experiments were subsequently completed with an underfeeding test. A cow (Egga 430, Fig. 13, that is, the same cow as

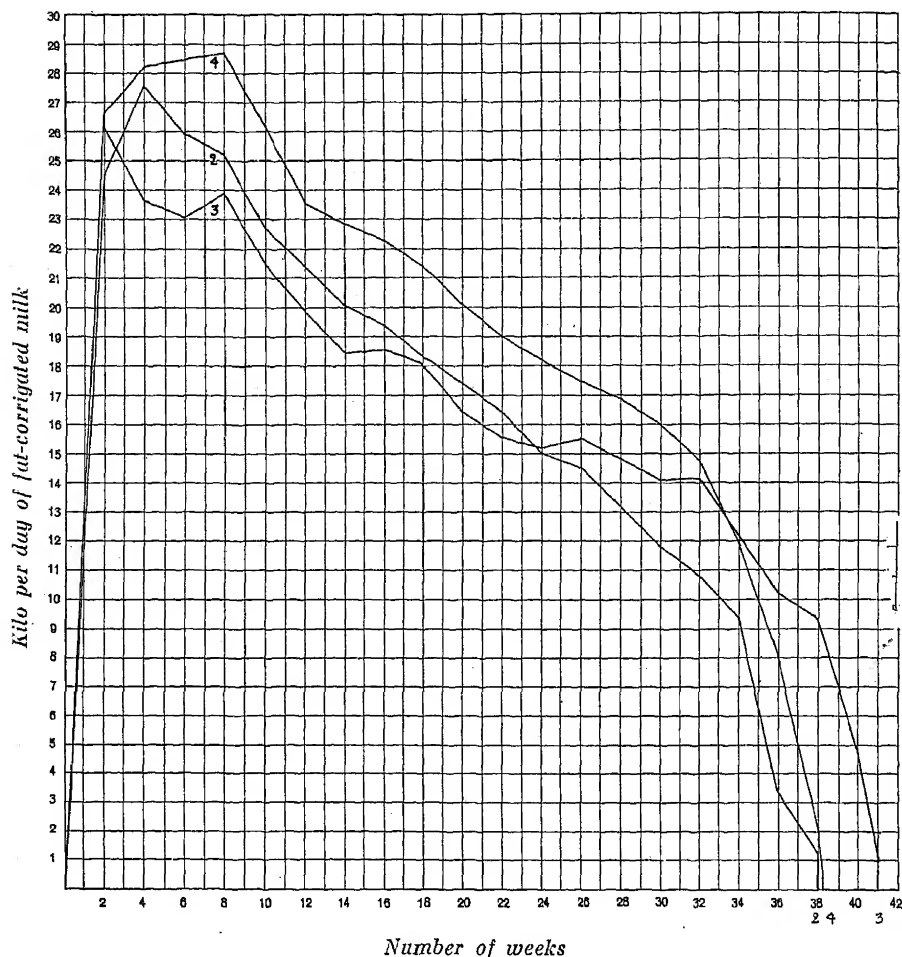


Fig. 6. Curves for the lactation years Nos. 2, 3 and 4 for the cow 804 Julia.

the one exemplified in Fig. 5) was given just at the beginning of her sixth lactation year a supply of feed which was equivalent to a much lower quantity of milk than that she might be expected to attain at the beginning of the lactation year. For a period of a little more than 8 weeks this cow was given a ration corresponding to only 17 kilos of fat corrigated milk per day whereas the maximum daily yield

attained by her in the preceding five lactation years amounted to between 26 and 28 kilos. By preventing the cow in this way from milking the full quantity which she would probably have produced otherwise, it was expected — in conformity with the views of certain breeders — that she would produce this »reserve» quantity of milk later on in the year when put out to graze and when she would thus be able to satisfy the whole of her requirement of feed. In this way it should be possible to obtain a lactation curve which ran a more horizontal course not only during the time the cow was being underfed but also afterwards. But

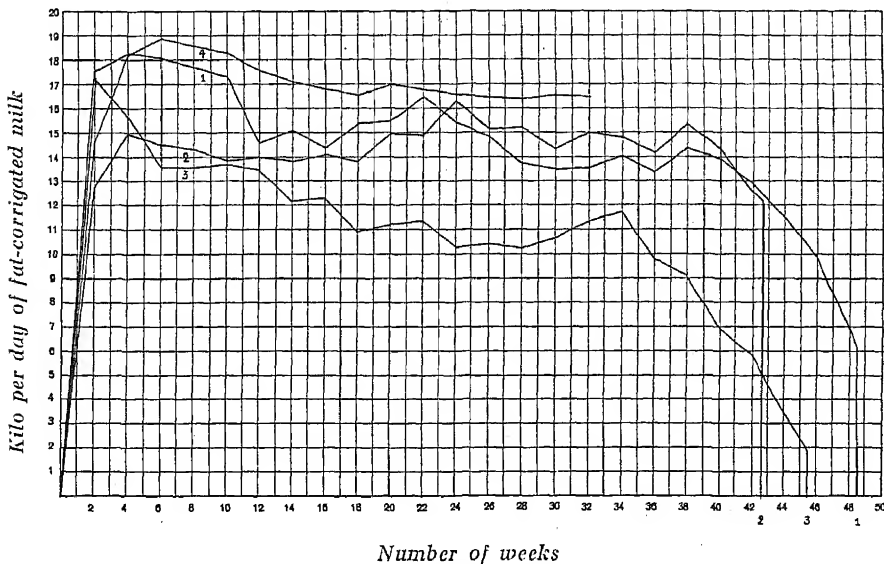


Fig. 7. Curves for the lactation years Nos. 1, 2, 3 and 4 for the cow 816 Marta.

as shown in Fig. 13 (cf. also Fig. 5, lactation year 6) the lactation curve again declined, when the cow was put out to graze after the 8 weeks' underfeeding, in the same manner as it had done in the previous years.

It should again be pointed out that in citing the above facts no claim is made that any positive proof is adduced that the shape of the lactation curve is constitutionally determined, and still less that it is genetically determined. But the facts mentioned appear to be so obvious that it should be worth while for investigators interested in these problems making a serious study of the genetics of those factors which may determine the shape of the lactation curve.

It would of course be well if we could find an appropriate

numerical measure by means of which the shape of the lactation curve could be characterized. But it is by no means certain that such a figure can be found. Among others, SANDERS' »Shape-figure» (SANDERS 1923) or FREDERIKSEN's figure »G» (FREDERIKSEN 1931) hardly seem to be satisfactory. In trying to find an appropriate figure it should first be

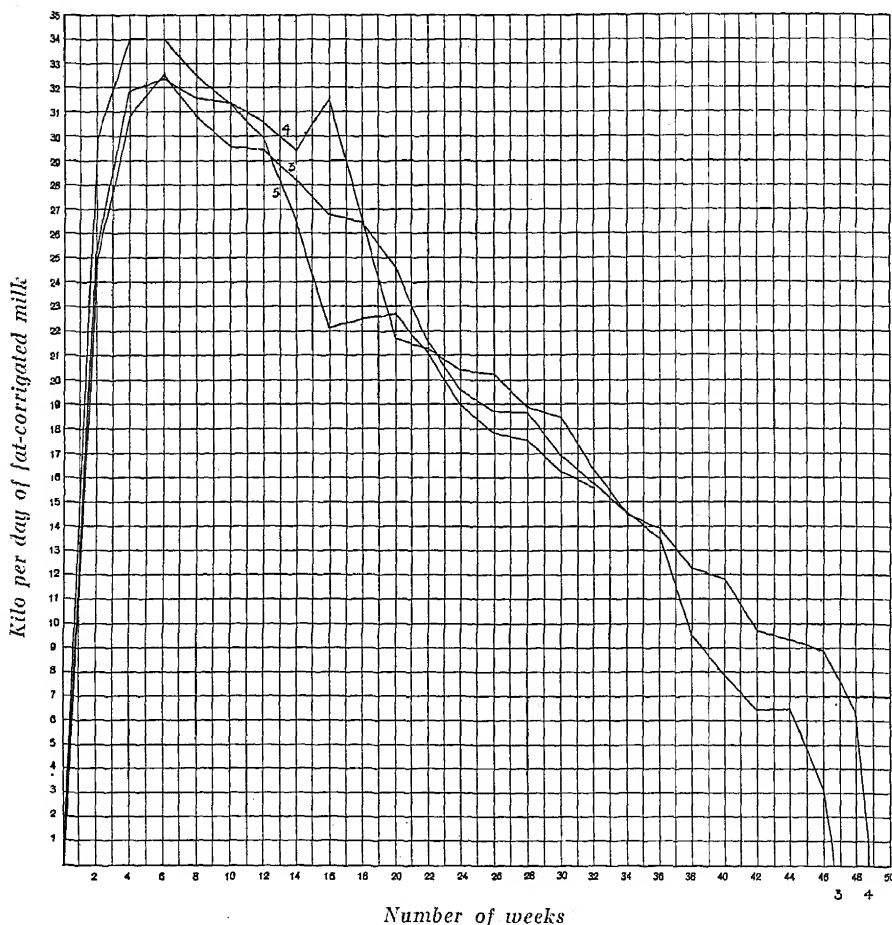


Fig. 8. Curves for the lactation years Nos. 3, 4 and 5 for the cow 626 Annita.

established *what* portion and *how large* a portion of the lactation curve is to be employed as the basis in computing the figure. The first question will then be whether for all lactation curves we shall start from exactly the same number of days after the birth of the calf or from the day on which the maximum yield has been attained. It may, however, be a matter of difficulty to determine the latter day, for it is

not unusual for a lactation curve to show several successive maxima at longer or shorter intervals. This is especially the case in lactation curves that run a rather horizontal course. On the whole it is probable that the majority of figures which may be considered from a theoretical point of view to be suitable as a measurement of the shape of the lactation curve will be too sensitive to the fluctuations, all too common,

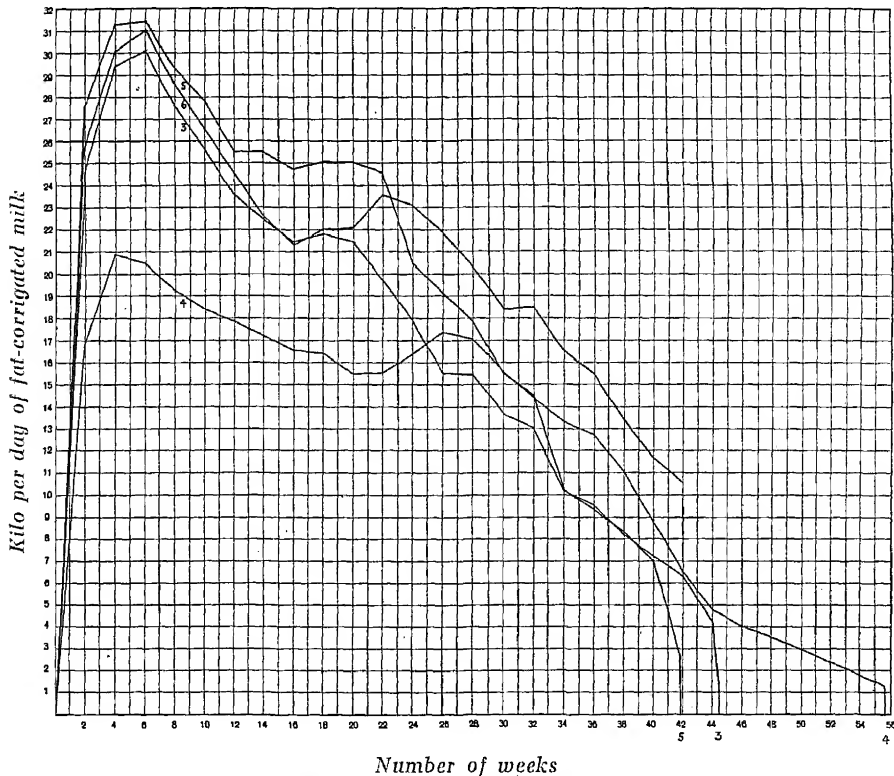


Fig. 9. Curves for the lactation years Nos. 3, 4, 5 and 6 for the cow 553 Ingeborg.

in the course of the lactation curve, and which may be caused by purely incidental occurrences.

For the lactation curves which run a fairly rectilinear course the linear regression coefficient constitutes a natural measurement of the shape of the lactation curve, that is, of its rate of decline. It may therefore be assumed that the linear regression coefficient may be used as a suitable measurement of the slope of the lactation curve, a certain part of the lactation curve being employed as the basis of the computation. How large this part of the lactation curve should be most

conveniently used is rather a difficult matter to decide. In the examples given below, which refer to the curves shown in Figs. 1—10, the regression coefficient for each curve has been computed in such a manner that the weekly average of fat corrigated milk has been employed as a unit, also that 13 weekly periods have been used and finally the week in which the maximum production was attained has been taken as the first period in each series. The reason why an uneven number of periods has been employed is that by this means the computations can be simplified. If we have  $(2h + 1)$  periods and these periods are numbered from the middle period (which is given the number 0) then we obtain the linear regression coefficient  $b$  from the formula

$$b = \frac{3S(km)}{h \cdot (h + 1) \cdot (2h + 1)}$$

where  $m$  denotes the weekly average of fat corrigated milk,  $k$  the number of the week (which is counted negatively backwards from the middle period), and where the summation is extended over all periods. For 13 periods, i. e. for  $h = 6$  the formula will be

$$b = \frac{S(km)}{182}$$

Using this formula as a basis we obtain the following linear regression coefficients:

Lactation year	1	2	3	4	5	6	7
458 Tita .....	—3,10	—4,12	—1,43				
740 Idun .....		—2,51	—2,55	—2,35	—3,37		
414 Dutty .....			—2,62	—2,23	—2,64	—2,19	—3,72
437 Åsa .....	—4,22	—4,08	—4,36	—5,46			
430 Egga .....		—7,52	—8,28	—5,45	—5,17	—2,75	
804 Julia .....		—5,26	—4,14	—4,13			
816 Marta .....	—2,96	—0,53	—2,39	—1,66			
626 Annita .....			—3,45	—3,35	—6,11		
553 Ingeborg .....			—5,81	—2,70	—3,65	—6,27	
663 Marta .....			—5,85	—4,51	—5,72		

These coefficients may at least partly be considered to give a measurement of the shape of the curves or more correctly a measurement of the rate of decline of the curves. For instance, if a comparison is made between the rapidly falling curve for 430 Egga (Fig. 5) and

the more even running curve for 414 Dutty (Fig. 3) or the still more level curve for 816 Marta (Fig. 7) it will be seen that the corresponding coefficients reflect fairly well the difference in the slope of the curves. With regard to the last lactation year for 430 Egga the coefficient here has a value far below those for the other lactation years. The explanation of this is very simple; this was the year in which the underfeeding test mentioned above was carried out.

That the method suggested here is far from perfect is readily

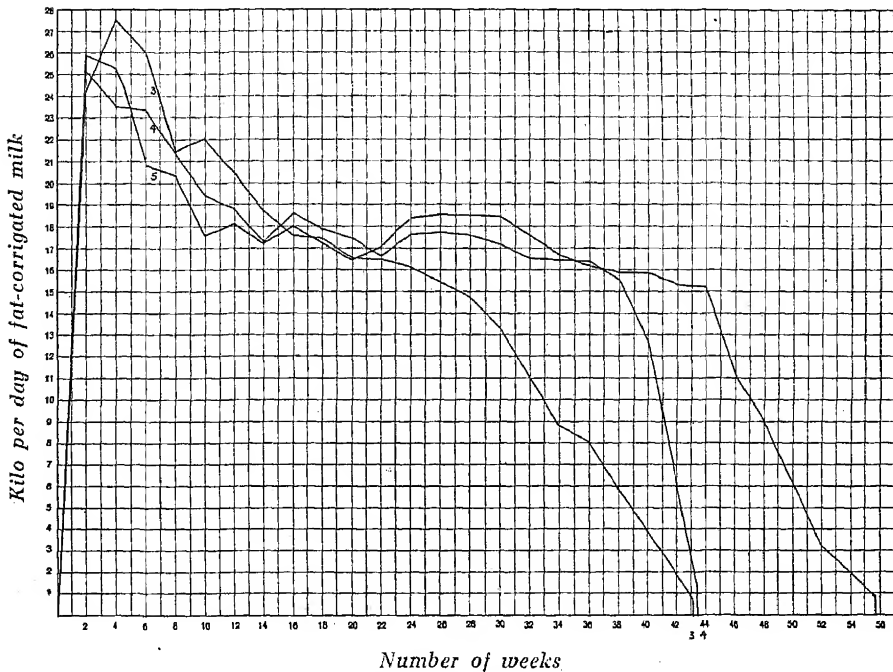


Fig. 10. Curves for the lactation years Nos. 3, 4 and 5 for the cow 663 Marta.

admitted: it is too sensitive to incidental variations in the course of the curves. Consider for instance Fig. 8! The three lactation curves reproduced in the figure undoubtedly run a very uniform course. But the incidental concavity in the last lactation curve brings about a great increase in the numerical value of the corresponding coefficient. An analogous effect on the coefficient caused by incidental circumstances can be pointed out in several other cases, and this should perhaps induce us to try to find a better measurement of the shape of the lactation curve. For instance, it might be possible to employ coefficients of a higher degree. Or it may be more convenient to



calculate the linear coefficient for different portions of the lactation curve. Different systems have been tested but none of them seems to furnish better results, for which reason they are not mentioned here.

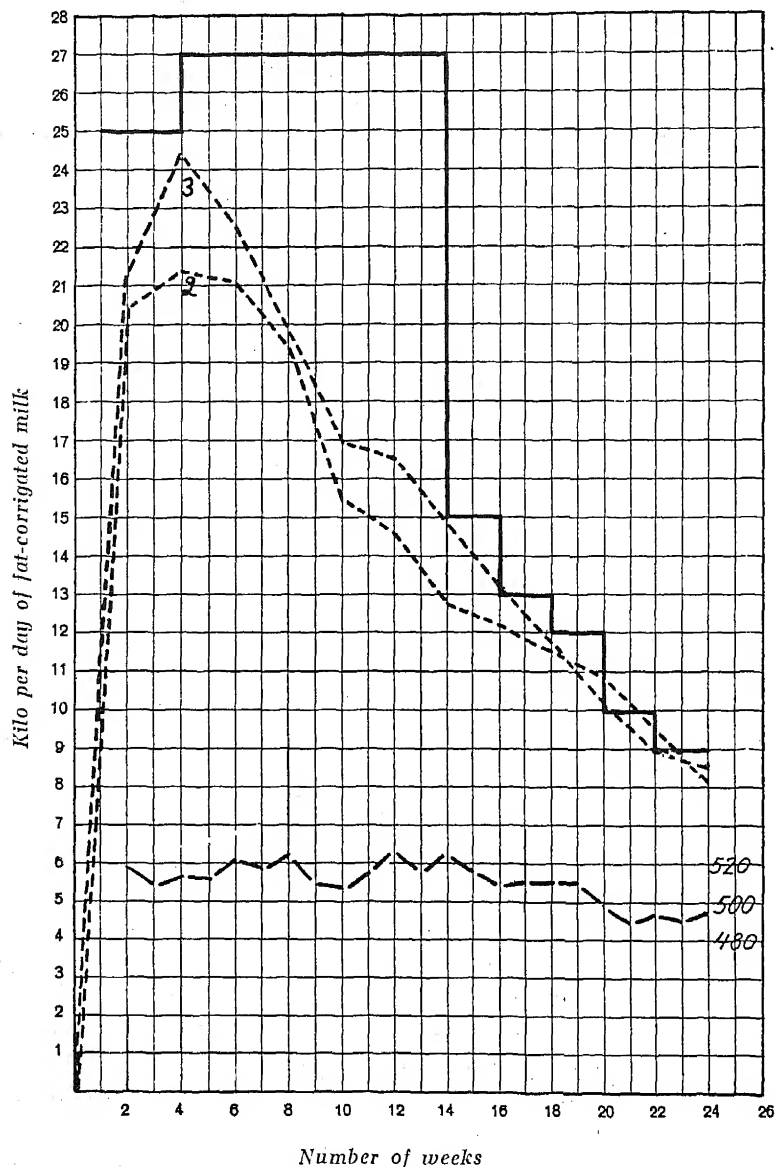


Fig. 11. Dotted lines: curves for the lactation years Nos. 2 and 3 for the cow 707 Kersti. — Heavy line: amount of fat-corrected milk for which food was given during lactation year No. 3. — Line below: weight in kilo.

It does not appear improbable either that the best measurement obtainable for a close analysis of the question of the genetic foundation of the shape of the lactation curve is the *visual measurement*, that is,

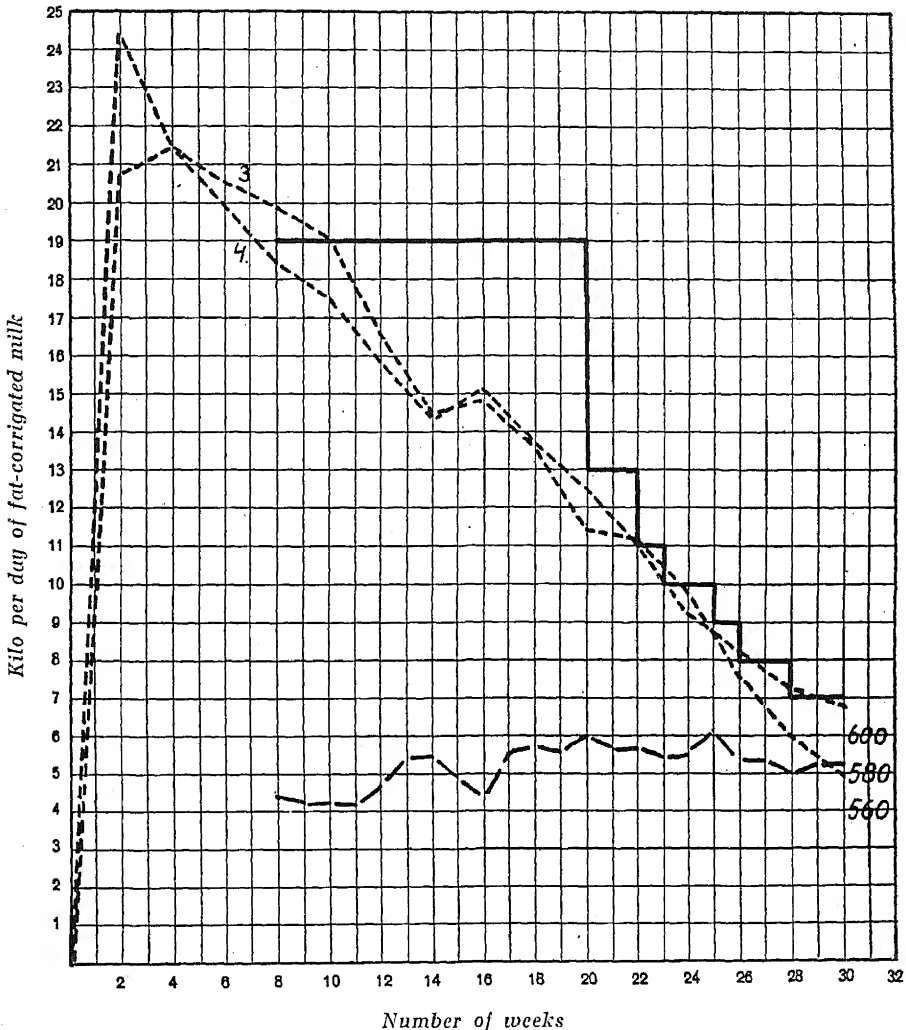


Fig. 12. Dotted lines: curves for the lactation years Nos. 3 and 4 for the cow 437 Åsa (same as in fig. 4). — Heavy line: amount of fat-corrected milk for which food was given during lactation year No. 4. — Line below: weight in kilo.

the one obtained in surveying the plotted curves. If it is pointed out that the numerical measurements employed vary too much for the different lactation years for each individual cow this does not imply

that evidence has been advanced to show that the shape of the lactation curve cannot be genetically conditioned; it signifies only that the numerical measurements employed were not quite adequate. The study of the possible hereditary character of the shape of the lactation curve must in that case be made without having recourse to any numerical measurements but must instead be effected by employing the visual impression made on the observer by the plotted curves.

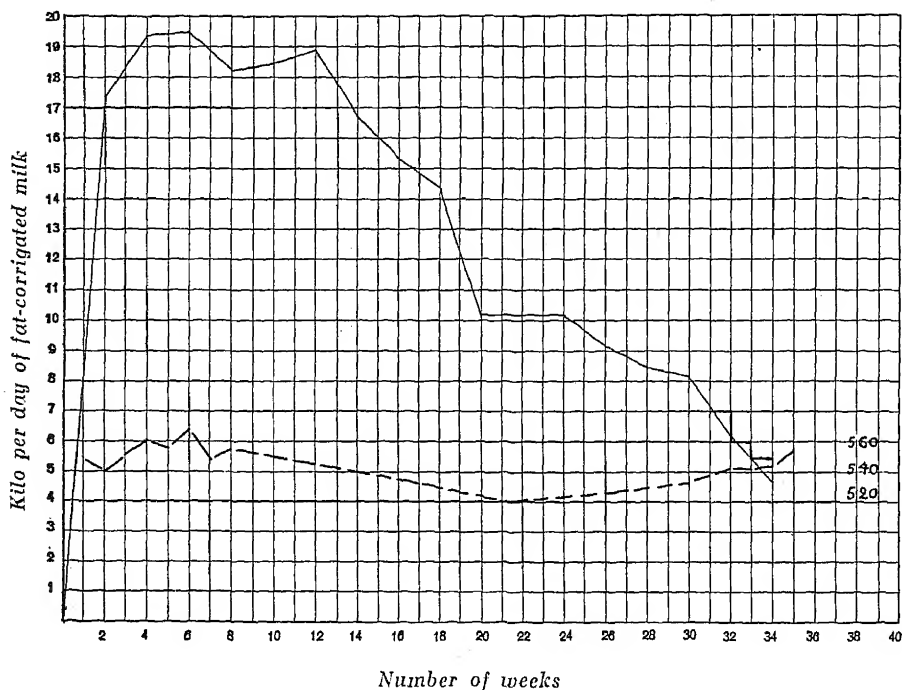


Fig. 13. Curve for the lactation year No. 6 for the cow 430 Egga (same as in fig. 5). — Horizontal line (at 17 kilos): amount of fat-corrigated milk for which food was given. — Line below: weight in kilo.

### SUMMARY.

1. A number of lactation curves corresponding to several lactation years has been reported here for 10 different cows. In conformity with what has already been pointed out by several writers attention has been called to the fact that the different lactation curves for the very same cow frequently exhibit a very great similarity in shape, whereas this shape varies considerably from cow to cow.

2. Owing to these circumstances it may be assumed that the shape

of the lactation curve is constitutionally conditioned and is consequently also determined genetically. This fact has also been pointed out by various investigators although no positive evidence in support of the theory has been adduced so far. This assumption is also supported to a certain extent by some experiments reported in the present paper, by means of which attempts were made to alter the shape of the lactation by feeding, but without success.

3. Attention has therefore been called to the necessity of seriously studying the question as to the possible hereditary nature of the shape of the lactation curve. As a suitable measurement of the shape of the lactation is required in these studies some possibilities have been discussed. Among others, a suggestion has been made as to the use of the linear regression coefficient, and this coefficient has been calculated for the lactation years shown in the curves.

4. It has also been pointed out, however, that these coefficients easily become too sensitive to incidental variations, and for that reason the best measurement is perhaps the visual picture obtained in surveying the curves.

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# ZUR KENNTNIS DER ZYTOLOGIE DER SKANDINAVISCHEN ANTENNARIA-ARTEN

VON BENGT BERGMAN

STOCKHOLM

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IM Sommer 1932 begann ich eine zytologische Untersuchung nicht nur über die skandinavischen *Antennaria*-Arten, sondern auch über einige amerikanische, die im Hortus Bergianus in Stockholm kultiviert werden. Schon Ende desselben Jahres erschienen jedoch zwei zytologische Arbeiten von STEBBINS (1932 a, b) über zehn nordamerikanische Antennarien, unter denen sich auch die von mir fixierten befanden. Ich habe mich daher im weiteren Verlaufe meiner Untersuchung auf die skandinavischen Arten beschränkt.

Sieben von den von STEBBINS untersuchten Antennarien waren apomiktisch nach dem *Antennaria*-Schema. Die zytologischen Verhältnisse bei den rein weiblichen Pflanzen waren für alle dieselben. In den EMZ kommen bei allen zwei Teilungsmodi vor. Dem einen, der der unvergleichlich gewöhnlichste ist, geht ein langdauerndes Ruhestadium voraus. Die darauf folgende Teilung ist rein mitotisch. Es konnten keine meiotischen Prophasenstadien nachgewiesen werden. »At the metaphase the chromosomes are all of the long, slender, somatic type and are arranged as in an ordinary somatic division» (STEBBINS 1932 b, S. 327). Bei dem anderen Teilungsmodus geht kein langdauerndes Ruhestadium voraus, sondern die Teilung erfolgt im gleichen Zeitpunkt wie bei nicht-apomiktischen Arten. Die meiotischen Prophasenstadien sind vorhanden. In der Diakinese und Metaphase sind die Chromosomen stark kontrahiert wie in einer gewöhnlichen Meiosis. Die Mehrzahl der Chromosomen ist aber unpaarig, weshalb wir eine Art semiheterotypischer Teilung erhalten. Die Folge dieser ist Polyadenbildung und Sterilität.

Dieser andere Teilungstypus kommt weniger oft und bei den verschiedenen Arten mit verschiedener Frequenz vor. So ist er bei einigen sehr selten, bei anderen dagegen kommt er in 20—25 % der Samenanlagen vor.

Unter den amerikanischen, apomiktischen *Antennaria*-Arten sind männliche Exemplare sehr selten oder unbekannt. Dasselbe gilt wie bekannt auch für die in Skandinavien vorkommenden apomiktischen

*A. alpina*. Von drei Arten gelang es STEBBINS, Material männlicher Pflanzen zu erhalten. Zwei waren nur durch den »abweichenden« Typus vertreten, den JUEL (1900, S. 12) für *A. alpina* beschreibt. Sie hatten also Samenanlagen in ihren Blüten. Die dritte bestand teils aus reinen Männchen, teils aus dem »abweichenden« Typus. In der Mikrosporogenese kommen sowohl Univalente wie Bivalente vor; bei *A. parlinii* möglicherweise auch Trivalente und Tetravalente. Nur bei *A. fallax* hat er die Teilungen in EMZ bei dem »abweichenden« Typus studiert. Die Chromosomen sind hier wie in einer gewöhnlichen Meiosis kontrahiert. In der ersten Teilung ist eine grosse Anzahl Univalente über die Spindel zerstreut. In PMZ dagegen waren nur »from two to twelve univalents . . . scattered over the spindle« (STEBBINS 1932 b, S. 322). Die Bindung ist in EMZ offenbar bedeutend schwächer als in PMZ.

### MATERIAL UND METHODE.

Diese Untersuchung umfasst *A. alpina* ♂ (L.) GÄRTN., *A. intermedia* (ROSENV.) PORR., *A. carpathica* (WG.) BL. & FING. und *A. dioica* (L.) GÄRTN. Von *A. alpina* ♂ und *A. intermedia* habe ich fixiertes Material von Herrn Dozent Dr. OTTO HEILBORN in Stockholm erhalten. Ich habe sie auch im Hortus Bergianus (Stockholm) fixiert, wo sie kultiviert werden. *A. carpathica* und auch *A. alpina* ♂ und ♀ sind im nördlichen Schweden (Abisko) von mir eingesammelt worden. *A. dioica* stammt aus der Umgegend Stockholms.

Als Fixierflüssigkeiten wurden NAWASHINS Chromsäure-Essigsäure-Formalin und CARNOYS Alkohol-Chloroform-Eisessig benutzt. Die Färbungen sind mit NEWTONS Gentiana-Violett und HEIDENHAINS Eisen-Alaun-Hämatoxylin ausgeführt worden.

### BEOBACHTUNGEN.

#### A. ALPINA ♂.

*Die Teilungen der PMZ.* — Von *A. alpina* ♂ habe ich hauptsächlich einen »abweichenden« Typus untersucht. Schon JUELS (1900) Beobachtung über das unregelmässige Aussehen der Pollenkörner deutet auf eine gestörte Meiosis in PMZ. Dies wird durch meine Untersuchung bestätigt. Die Anzahl der univalenten Chromosomen ist jedoch nicht so beträchtlich hoch. Gewöhnlich findet man 4—12 in der Spindel zerstreut, und *A. alpina* ♂ erinnert diesbezüglich sehr an *A. fallax* ♂ (STEBBINS 1932 b, S. 322). Dagegen kommen viele Bi- und Multi-

valente vor. Da die Chromosomenzahl bei *A. alpina* sehr hoch ist ( $2n = 84$ , siehe unten), ist es sehr schwer, die Bindungsverhältnisse zu studieren. Besonders gilt dies für die Metaphasen, in denen die

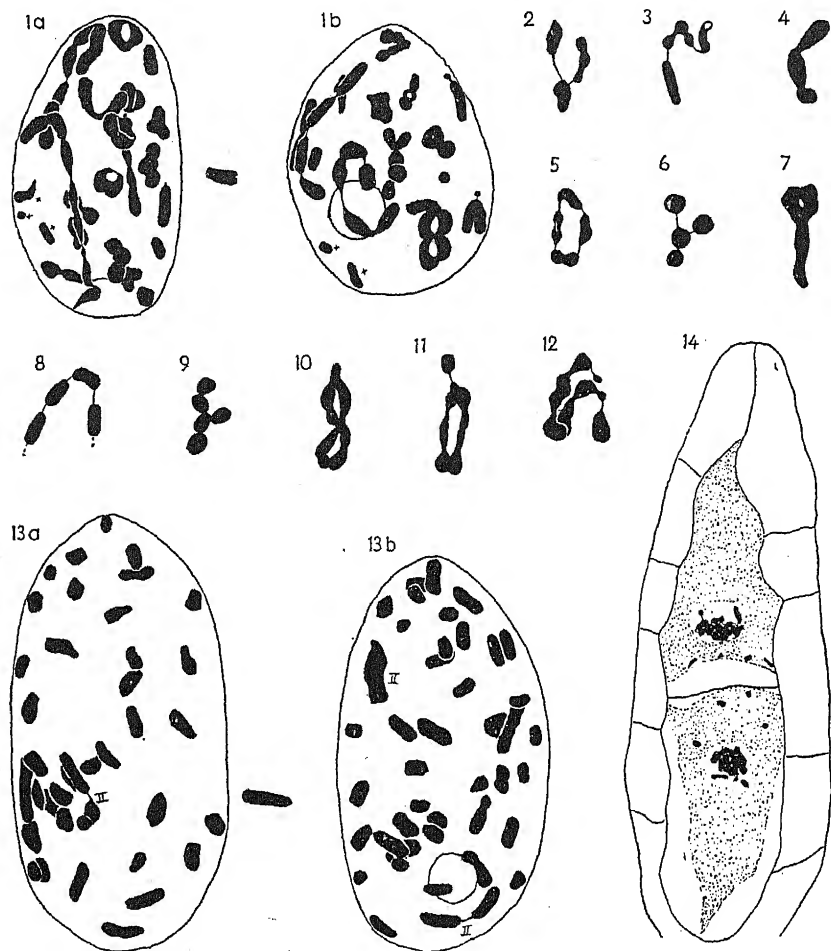


Fig. 1—14. *Antennaria alpina* ♂. »Abweichender» Typus. — Fig. 1. PMZ in Diakinese. — Fig. 2—12. Multivalente aus verschiedenen Metaphasen und Diakinesen freigelegt. — Fig. 13. EMZ in Diakinese. — Fig. 14. Die EMZ hat ihre erste Teilung durchgemacht, und die zweite bereitet sich vor. —

Fig. 1—13,  $\times 2150$ ; Fig. 14,  $\times 840$ .

Chromosomen sich gern zusammenklumpen, weshalb es nur in gewissen, besonders günstigen Teilen der Metaphasenplatten möglich ist, die Konnexen zu verfolgen. In ihrer Gesamtheit machen die Metaphasen jedoch den Eindruck einer hochgradigen Bindung. Die Diakinesen sind

aber besser zu beobachten, und eine solche, von dem Messer in zwei Schnitte zerlegt, ist in Fig. 1 *a* und *b* gezeichnet. Hier kommen wahrscheinlich folgende Bindungen vor: 1 Hexavalent, 4 Pentavalente, 2 Tetravalente, 2 Trivalente, 16 Bivalente und 9 Univalente. Da mit einem  $\times$  zerschnittene Chromosomen bezeichnet worden sind, ist die somatische Zahl offenbar höher als 80.

In Fig. 2—12 ist eine Anzahl Multivalente aus verschiedenen Metaphasen und Diakinesen freigelegt. Fig. 2—4 zeigen Trivalente, Fig. 5—7 Tetravalente. Fig. 8 stellt eine Kette von mindestens vier Chromosomen dar. Sie ragte aus einer Metaphasenplatte hervor, aber ihr weiteres Aussehen war nicht festzustellen. Fig. 9 und 11 sind Pentavalente. Fig. 10 ist entweder eine Tetra- oder Pentavalent, Fig. 12 wahrscheinlich ein Hexavalent.

Ungefähr dasselbe Aussehen hat die Meiosis bei den reinen Männchen.

*Die Teilungen der EMZ.* — Bei dem von mir untersuchten Männchen von »abweichendem« Typus kommen Samenanlagen in den meisten Blüten vor. Der ersten Teilung der EMZ geht kein langdauerndes Ruhestadium voraus. Ein »Synapsisstadium« kommt vor. Die Chromosomen sind stark kontrahiert. In der Diakinese treten aber im Gegensatz zu dem Verhalten in PMZ fast alle Chromosomen unpaarig auf. Dies geht aus Fig. 13 hervor. Sie stellt eine Diakinese in zwei Schnitten dar. 78 Univalente und 3 Bivalente, von denen zwei sehr schwache Konnexen haben, sind vorhanden. Die somatische Zahl ist demnach 84. Die folgende Metaphase-Anaphase ist fast rein semi-heterotypisch mit gewöhnlich darauf folgender Polyadenbildung. In Fig. 14 bereitet sich die zweite Metaphase vor. Eine Anzahl bei der ersten Teilung zurückgelassene Chromosomen liegen im Plasma zerstreut.

Diese Teilung stimmt mit jener überein, die STEBBINS in EMZ der Männchen von *A. fallax* beschrieben hat. Sie ist offenbar identisch mit dem anderen Typus, dem (semi-)heterotypischen, der bisweilen bei den apomiktischen *Antennaria*-Weibchen vorkommt (»the second type«, STEBBINS, 1932 b, S. 328).

In *A. alpina* ♂ habe ich niemals die Entwicklung eines Embryosacks gesehen. Die Samenanlagen stellen ihr Wachstum in einem jungen Stadium ein und sind immer steril.

In rein weiblichen Exemplaren habe ich keine Teilungen der EMZ untersucht. STEBBINS hat das Verdienst diese Sache bei den apomiktischen *Antennarien* aufgeklärt zu haben. Seine Ergebnisse gelten sicher



auch für *A. alpina* ♀. Aus JUELS (1900) Untersuchung geht hervor, dass auch hier die beiden Teilungsmodi [der »mitotische« und der (semi-)heterotypische] vorkommen. So bezieht sich seine Fig. 24, Taf. VI, auf die »mitotische« und Fig. 25, Taf. VI auf die (semi-)heterotypische. Diese zwei Teilungen wurden, wie bekannt, von JUEL (1900) zu einem einzigen Teilungstypus kombiniert, was nunmehr nicht als richtig betrachtet werden kann. Die heterotypische Teilung in Fig. 25, Taf. VI, in JUELS Arbeit ist offenbar von derselben Natur wie meine Fig. 13 und STEBBINS' (1932 b) Fig. 8—11, 40—41, 44—45 und 48. Wie bei unseren Untersuchungen kann die in Frage kommende Teilung nicht als eine »pseudohomotypische« (GUSTAFSSON 1934 a, b, 1935) aufgefasst werden, sondern wird zu Polyadenbildung und Sterilität führen, sofern nicht Restitutionskernbildung eintritt. Als eine weitere Stütze für diese Auffassung kann hier auf die Untersuchung HABERLANDTS (1923) über die erste Teilung der EMZ bei *A. alpina* ♀ hingewiesen werden. In den allermeisten Fällen fand er, dass der Teilung der EMZ ein langdauerndes Ruhestadium vorausgegangen war. Als diese Teilung endlich eintrat, fand er oft Stadien von dem Aussehen, das JUEL (1900) in Taf. V, Fig. 4 wiedergegeben hat, d. h. dasselbe Bild wie STEBBINS' Fig. 2 von *A. petaloidea* und BERGMANS (1935) Fig. 6 B von *Hieracium umbellatum*. Diese Teilung bezieht sich offenbar auf den ersten Teilungstypus bei *Antennaria*, dem »mitotischen«. Dass auch der andere Teilungstypus, der (semi-)heterotypische, angetroffen wurde, geht aus der folgenden Äusserung HABERLANDTS hervor (S. 288): »Bemerkenswert ist, dass in einzelnen Köpfchen der von mir untersuchten Form hin und wieder auch Samenanlagen auftraten, deren Embryosackmutterzellen sich genau so verhalten wie die von *A. dioica*, d. h. schon frühzeitig Tetradenteilung eingingen. In diesem Falle waren nach der vollzogenen Teilung die Nucelluszellen noch am Leben. Ihre Degeneration setzte erst ein, wenn die basale Zelle, zum Embryosack werdend, die drei anderen zu verdrängen begann (Fig. 5)«. Wenn man aber HABERLANDTS Fig. 5 studiert, findet man hier eine deutliche Pentade. Dieser Teilung geht also kein langdauerndes Ruhestadium voraus, und das Ergebnis ist Polyadenbildung. Dass diese Teilung von derselben Natur wie die in JUELS Fig. 25, Taf. VI, gewesen ist, d. h. ± semiheterotypisch, darüber kann wohl kaum ein Zweifel herrschen.

GUSTAFSSON (1934 a, b, 1935) will die »pseudohomotypische« Teilung den meisten apomiktischen Kompositen zuerkennen, geht aber dabei zu weit. Ohne Zweifel kommt sie bei *Erigeron*, *Taraxa-*

*cum* und wahrscheinlich auch bei *Chondrilla* vor. [Vielleicht auch bei *Ixeris* (*Lactuca*) *dentata* (OKABE, 1932), die übrigens eine interessante Zwischenstellung zwischen *Erigeron* und *Taraxacum* dadurch einnimmt, dass sie ephemere Zellplatten zwischen den ersten Tochterkernen ausbildet]. Bei *Antennaria*, *Eupatorium* und *Hieracium* dagegen werden die fertilen Embryosäcke im allgemeinen durch eine Äquationsteilung mit »mitotisierten« Chromosomen geliefert.

Die somatische Chromosomenzahl bei *A. alpina* wird von JUEL (1900) zu 48—52 angegeben. Diese Zahl ist jedoch viel zu niedrig, was darauf beruht, dass JUEL die heterotypische Metaphase in Fig. 25, Taf. VI, fehlerhaft gedeutet hat (JUEL 1900, S. 21). In dieser Figur können 84 univalente Chromosomen gezählt werden, was in gutem Einklang mit meiner Fig. 13 steht. Bei *A. alpina* ist also  $2n = 84$ . In Wurzelspitzen habe ich sowohl bei männlichen wie bei weiblichen Pflanzen ungefähr 80 Chromosomen feststellen können. In Fig. 19 ist eine somatische Metaphasenplatte aus dem Wurzelmeristem eines »abweichenden« Männchens gezeichnet. 83 Chromosomen sind zu erkennen.

#### A. INTERMEDIA.

Soviel ich weiss, ist *A. intermedia* nur einmal in Skandinavien angetroffen worden (FRIES 1919). Das Material dieser Untersuchung stammt von grönländischen Pflanzen, die im Hortus Bergianus angepflanzt sind. Habituell stimmt *A. intermedia* mit *A. alpina* ♂ sehr nahe überein. Alle Exemplare, die ich untersucht habe, waren jedoch rein weiblich.

*Die Teilung der EMZ.* — In EMZ ist kein »Synapsisstadium« beobachtet worden. Das Ruhestadium des Kerns dauert sehr lange. Obgleich die EMZ schon stark vakuolisiert und der Nucellus grösstenteils degeneriert ist, befindet sich der Kern noch immer in Ruhe, was aus Fig. 15 ersichtlich ist. Die Teilung tritt erst in dem Stadium ein, das ich für eine apomiktische Form von *Hieracium umbellatum* neulich angegeben habe (BERGMAN 1935, S. 58). Aus Fig. 16 geht hervor, dass sie rein somatisch mit langen mitotischen Chromosomen ist. Es ist also klar, dass auch *A. intermedia* diplo-parthenogenetisch nach dem *Antennaria*-Schema ist.

Die weitere Entwicklung und Ausbildung des Embryosacks geschieht in derselben Weise, wie JUEL (1900) und STEBBINS (1932 b) es für andere apomiktische Antennarien angegeben haben. Embryobildung tritt in der Regel ein, obgleich keine Männchen vorhanden waren.

Um die somatische Chromosomenzahl bei *A. intermedia* festzustellen, habe ich mehrere Wurzelspitzenfixierungen gemacht. Es erwies sich aber als unmöglich, gute Fixierungen zu erhalten, weshalb ich leider keine sicheren Angaben über die Chromosomenzahl liefern kann.

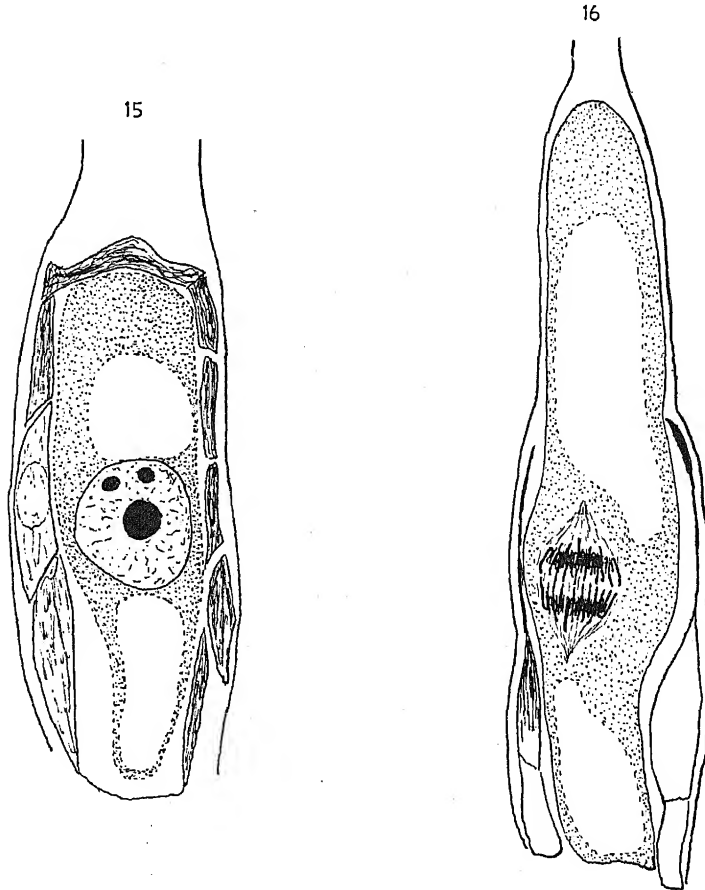


Fig. 15—16. *Antennaria intermedia*. — Fig. 15. Die EMZ ist direkt in einen einkernigen Embryosack umgewandelt. Der Kern im Ruhestadium. — Fig. 16. Der Kern macht seine erste Teilung durch. Sie ist rein somatisch mit langen, mitotischen Chromosomen. —  $\times 1120$ .

Sie scheint aber sehr hoch zu sein und ist wahrscheinlich dieselbe wie bei *A. alpina*.

So wie die Dinge bei *A. intermedia* liegen, ist sie wohl nur als eine Form von *A. alpina* aufzufassen.

## A. CARPATHICA UND DIOICA.

Für *A. carpathica* und *A. dioica* habe ich eigentlich nur die somatischen Chromosomenzahlen mitzuteilen. Die Körbchen, die ich von *A. carpathica* fixiert hatte, waren zu alt, um die Mikrosporogenese zu ermitteln. Merkwürdigerweise fand ich in meinem Material in den alten Samenanlagen niemals Embryonen sondern nur stark angeschwollene und degenerierte Embryosäcke. Da überdies in den Antheren oft Zwergpollen anzutreffen war, ist diese Pflanze einer eingehenderen Untersuchung wert. Ich hoffe mein Material in einem anderen Jahre ergänzen zu können.

Eine somatische Chromosomenplatte von *A. carpathica* ist in

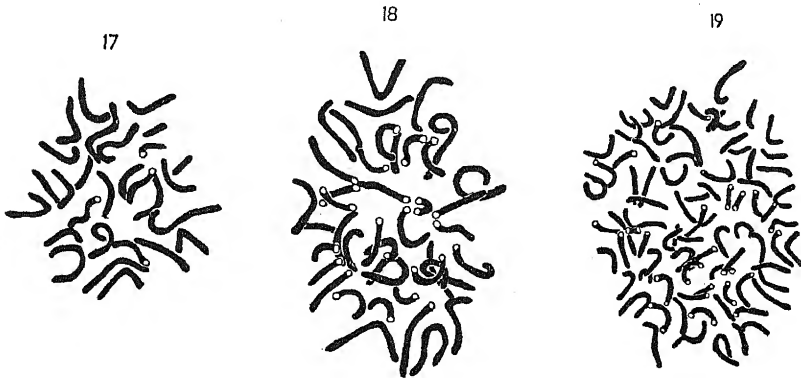


Fig. 17—19. Somatische Metaphasenplatten. — Fig. 17. *Antennaria dioica*. — Fig. 18. *Antennaria carpathica*. — Fig. 19. *Antennaria alpina*. —  $\times 2150$ .

Fig. 18 abgebildet. 41 Chromosomen sind zu erkennen. Die somatische Zahl liegt demnach zwischen 40 und 42. Wie es scheint, sind die Chromosomen von *A. alpina* (Fig. 19) ein wenig kürzer und dünner, was wahrscheinlich mit der hohen Zahl im Zusammenhang steht.

Für *A. dioica* liegen in der Literatur zwei Angaben über die Chromosomenzahl vor. JUEL (1900) gibt  $n = 12-14$  und HOLMGREN (1919)  $n = 13$  an. In Wurzelspitzen habe ich 28 Chromosomen gezählt, was aus Fig. 17 hervorgeht. Die somatische Zahl ist also 28, wie für die sexuellen *A. neglecta*, *A. plantaginifolia* und *A. solitaria* (STEBBINS, 1932 a).

Unter den Chromosomen von *A. dioica* sind zwei besonders klein. (Fig. 17.) Es ist möglich, dass sie Geschlechtschromosomen sind, aber ich habe dies noch nicht entscheiden können. Die Chromosomenplatte in Fig. 17 stammt von einem Individuum her, das ich zusammen mit

einigen anderen in Töpfe gepflanzt habe. Mit Ausnahme von einem hatten sie alle dieselbe Chromosomengarnitur, da sie aber noch nicht geblüht haben, kann nichts über die Geschlechtsverhältnisse ausgesagt werden. Das abweichende Individuum hatte merkwürdigerweise 34 Chromosomen, von denen 5 von derselben Grössenordnung wie die zwei kleinsten in Fig. 17 waren. Über diese Dinge will ich später berichten.

### DISKUSSION.

Eine hervorragende Frage der Apomixisforschung ist, wie die Apomikten ursprünglich entstanden sind. Schon JUEL (1900, S. 14) glaubte, dass *A. alpina* ein Artbastard sei, und dass sie möglicher-

TABELLE 1.

	Fortpflanzung	Somatische Chromosomenzahl	Autoren
<i>A. neglecta</i> .....	Sexuell	28	STEBBINS (1932 a)
<i>A. plantaginifolia</i> ...	»	28	»
<i>A. solitaria</i> .....	»	28	»
<i>A. dioica</i> .....	»	28	Verf.
<i>A. carpathica</i> .....	»	40—42	»
<i>A. fallax</i> .....	Apomiktisch	84	STEBBINS (1932 b)
<i>A. parlinii</i> .....	»	84	»
<i>A. canadensis</i> .....	»	83—86	»
<i>A. occidentalis</i> .....	»	75—85	»
<i>A. petaloidea</i> .....	»	75—80	»
<i>A. neodioica</i> .....	»	ca. 52	»
<i>A. brainerdii</i> .....	»	42	»
<i>A. alpina</i> .....	»	84	Verf.
<i>A. intermedia</i> .....	»	ca. 80 (?)	»

weise eine Kreuzung zwischen *A. dioica*  $\times$  *carpathica* oder *A. dioica*  $\times$  *monocephala* darstellen könnte. *A. carpathica* weicht aber so sehr von *A. alpina* ab, dass sie wohl in diesem Falle nicht in Frage kommen kann. Gegen diese Kombination sprechen auch die Chromosomenzahlen der beiden Arten. Die Chromosomenzahl von *A. monocephala* ist noch nicht bekannt, aber sie muss somatisch 140 oder 56 betragen, um in der Kombination *A. dioica*  $\times$  *monocephala* 84 Chromosomen geben zu können. Sollte sie 56 betragen, so müssen wir eine Verdoppelung nach der Befruchtung annehmen.

In der Gattung *Antennaria* sind die Chromosomenzahlen der

sexuellen Arten sehr niedrig, wie im allgemeinen in apomiktischen Gattungen. Wie aus Tabelle 1 hervorgeht, haben vier  $2n = 28$  und nur eine (*A. carpathica*)  $2n = 40-42$ . Von den neun apomiktischen haben sieben  $2n = \text{ca. } 80$ , eine  $2n = \text{ca. } 52$  und eine  $2n = 42$ . Da es auf Grund dieser Verhältnisse unwahrscheinlich ist, dass sexuelle Arten mit so hohen Zahlen wie 80 vorkommen, müssen wir damit rechnen, dass wenigstens diese Zahl durch Verdoppelung nach der Befruchtung entstanden ist. Ob dies im Zusammenhang mit einer Bastardierung stattgefunden hat oder nicht, ist in den einzelnen Fällen sehr schwer zu entscheiden (vgl. STEBBINS, 1932 b, S. 338—339). STEBBINS aber neigt überhaupt dazu, eine Bastardierung anzunehmen. Dies ist wohl auch in gewissen Fällen möglich, aber in anderen ist meiner Meinung nach Autopolyploidie wahrscheinlicher. Besonders gilt dies für *A. fallax*, bei der eine bemerkenswert gute Bindung und auch Multivalentenassoziationen vorhanden sind. Da ferner »*A. fallax* differs from *A. plantaginifolia* only in its larger size throughout, and higher chromosome number» (STEBBINS, 1932 b, S. 338), ist sie vermutlich nur eine hexaploide Form von *A. plantaginifolia*.

Bei *A. alpina* deutet die gute Bindung und Multivalentenbildung in PMZ auf sechs homologe Genome. Sie ist darum am ehesten als eine Autohexaploide aufzufassen. Wie sie ursprünglich entstanden ist, ist aber schwieriger zu sagen. Wegen ihrer grossen Ähnlichkeit mit *A. dioica* ist es jedoch nicht unmöglich, dass sie aus einer *dioica*-ähnlichen Form durch Kopulation einer haploiden mit einer diploiden Gamete und darauffolgender Längsspaltung der Chromosomen in der jungen Embryoinitialzelle entstanden ist. Wie oben gesagt, müssen wir jedenfalls mit grösster Wahrscheinlichkeit mit einer Chromosomenverdoppelung nach der Befruchtung rechnen, um die höchsten Zahlen in *Antennaria* zu erklären.

Eine andere Frage der Apomixisforschung ist die, wie der Polymorphismus bei den Totalapomikten entsteht. Seit aber DARLINGTON (1932, S. 472—474) nachgewiesen hat, dass bei diplo-parthenogenetischen Pflanzen sehr wohl eine Spaltung vorkommen kann, die der bei den sexuellen entspricht, haben wir vermutlich die Lösung dieses Problems erhalten. Die Voraussetzung einer solchen Spaltung ist, dass wenigstens ein Chromosomenpaar in EMZ konjugiert (sodass die Möglichkeit eines »crossing-over« vorliegt), und dass dann Restitutionskernbildung folgt. Da wir aus STEBBINS' Untersuchung wissen, dass die »mitotische« Teilung in EMZ mitunter durch eine (semi)-heterotypische ersetzt wird, sind diese beiden Voraussetzungen bei den diplo-partheno-

genetischen Antennarien vorhanden. Dasselbe habe ich neulich für eine apomiktische Form von *Hieracium umbellatum* nachgewiesen (BERGMAN 1935, S. 59—60). Wenigstens bei *Antennaria* und *Archieracium* ist es sehr wahrscheinlich, dass eine solche Spaltung die hauptsächlichste Ursache des Polymorphismus ist.

Die meiner Meinung nach autopolyploide Natur von *A. alpina* hat natürlich zur Folge, dass sie nicht dieselben Voraussetzungen für eine Spaltung hat wie eine Allopolyploide. Da aber die wildwachsenden, sexuellen Arten wenigstens bei *Antennaria* heterozygot sind, und da *A. alpina* aus einer solchen entstanden sein muss, so ergibt sich, dass ihr solche Voraussetzungen nicht fehlen können. Wir kennen auch seit langem viele Varietäten von *A. alpina*, die Spaltungsprodukte sein können. *A. intermedia* ist vermutlich auch eine solche.

Ein altes Problem ist das Vorkommen von *A. alpina* ♂. Am einfachsten ist es, hier das Männchen in Analogie mit den obgenannten Varietäten als ein Spaltungsprodukt der Weibchen aufzufassen.

GUSTAFSSON (1934 a, 1935) hat kürzlich eine andere, interessante Abspaltungstheorie für Totalapomikten aufgestellt. Diese Theorie setzt aber eine »pseudohomotypische« Teilung mit »Fehlgehen der Chromatiden« in den »Pseudogemini« voraus. Weder STEBBINS noch ich haben eine solche Teilung bei *Antennaria* gesehen. Ich will aber damit nicht gesagt haben, dass eine »pseudohomotypische« Teilung (eine Äquationsteilung mit meiotisch kontrahierten Chromosomen) nicht vereinzelt vorkommen könnte [vielleicht ist Fig. 4 in STEBBINS' (1932 b) Arbeit eine solche?], aber sie muss dann sehr selten sein, und es kann ihr kaum eine Bedeutung bei *Antennaria* zukommen. Ich will noch einmal hervorheben, dass bei *Antennaria* und *Archieracium* (wenigstens in der von mir untersuchten Form) die fertilen Embryosäcke in den allermeisten Samenanlagen durch eine »mitotische« Teilung geliefert werden. Die fertilen Embryosäcke, die mitunter durch eine (semi-)heterotypische Teilung und Restitutionskernbildung entstehen, sind für die Fortpflanzung von geringerer Bedeutung, für die Formenbildung aber wahrscheinlich von grösstem Wert.

Sehr bemerkenswert ist, dass in EMZ sowohl von reinen Weibchen als von Männchen vom »abweichenden« Typus fast keine Chromosomenbindung vorhanden ist, trotzdem eine grosse Menge homologer Chromosomen vorkommt, was aus der Mikrosporogenese hervorgeht. Dieselbe Sache hat auch GUSTAFSSON (1935) in *Taraxacum* gefunden.

Weder STEBBINS noch ich haben in EMZ der *Antennaria*-Männchen

vom »abweichenden« Typus die Verspätung der ersten Teilung mit der folgenden »Mitotisierung« der Chromosomen gesehen. Diese Eigenschaft, die für die reinen Weibchen so charakteristisch ist, muss wahrscheinlich genenbedingt und geschlechtsgekoppelt sein.

### ZUSAMMENFASSUNG.

1. In der Mikrosporogenese von *A. alpina* ♂ kommt hochgradige Bindung und Multivalentbildung vor. *A. alpina* ist darum wahrscheinlich autohexaploid.

2. Von den zwei Teilungsmodi in EMZ der reinen Weibchen, des »mitotischen« und des (semi-)heterotypischen, kommt nur der letztere in EMZ der »abweichenden« Männchen vor. Die »mitotische« Teilung der reinen Weibchen muss wahrscheinlich genenbedingt und geschlechtsgekoppelt sein.

3. In der (semi-)heterotypischen Teilung der EMZ bei den Männchen vom »abweichenden« Typus wie auch bei den reinen Weibchen liegt fast vollkommene Asyndese vor, trotzdem eine grosse Menge homologer Chromosomen vorhanden sein muss.

4. Die Männchen von *A. alpina* werden wahrscheinlich von den Weibchen im Zusammenhang mit einer (semi-)heterotypischen Teilung und Restitutionskernbildung in EMZ abgespaltet. (Laut DARLINGTONS Abspaltungstheorie für diplo-parthenogenetische Pflanzen.)

5. *A. intermedia* ist diplo-parthenogenetisch nach dem *Antennaria*-Schema.

6. Folgende somatische Chromosomenzahlen sind nachgewiesen worden: *A. alpina*  $2n = 84$ , *A. intermedia*  $2n = \text{ca. } 80$  (?), *A. carpathica*  $2n = 40-42$ , *A. dioica*  $2n = 28$ .

Stockholm, Botanisches Institut der Universität, Oktober 1934.

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# THE PROBLEM OF THE ORIGIN OF SPECIES SINCE DARWIN

BY HERIBERT NILSSON

LUND

(Inauguration Address delivered at Lund University on April 14th, 1934)

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WHEN DARWIN sought an explanation of biological evolution, the progressive development from unicellular organisms to man, he found it in three factors: variation, heredity, and the struggle for existence. That plant and animal species were polymorphous he discovered by investigating various species, particularly domestic animals and cultivated plants. That the differences observed were hereditary was proved by the fact that they were not eliminated if the interrelated different varieties were brought up under exactly the same external conditions. And finally, DARWIN was able to ascertain that an enormously greater number of organisms were produced than there was subsistence to go round. This resulted in a mowing down and at the same time a sifting, whereby the less fit were eliminated while the better fitted survived. Evolution progressed onwards towards a higher and higher organization and perfection by means of this natural selection. The chain of evidence appears to be conclusive and complete.

But if we think of the matter a little more closely we shall see that this view of evolution has a weak point, and this did not escape DARWIN himself. And it is this: How do varieties arise then? They *exist*, very well, but how do new varieties *occur*? They breed true, how can they then vary? But vary they must if evolution is to advance. *Heredity and variation seem to be in an insolvable state of conflict with each other.*

To escape this difficulty DARWIN was driven from his theory of selection to a view advanced by his precursor as regards the evolutionary theory, that is, LAMARCK. Half a century before DARWIN a theory of evolution had been put forward by LAMARCK, and the driving force in the change of organisms he assumed to be the external conditions, the surroundings, the environment. The environment impressed its stamp on the organism, the organism adapted itself to the environment. Acquired characters became transmissible. Herein lay the motive of the change.

DARWIN, who had previously held that environment did not play any part in the evolutionary process, at last fell right into the arms of LAMARCK. He advanced a theory, to which has been given the name DARWIN's pangenesis theory. According to this theory there are hereditary carriers, pangenes, which are carried by the blood stream to the sexual organs and the sex cells. Here we have the explanation of heredity. But if a certain organ, on account of changed external conditions, acquires a stronger function and greater development these pangenes may be increased, be multiplied, and they are also transmitted to the sex cells in this multiplied form. Hence, the progeny also obtains this organ more powerfully developed. A new variety is formed. *Thus, acquired characters have become hereditary, also according to DARWIN.*

It is about this point that the battle has first been waging since DARWIN. Are then acquired characters hereditary or are they not? Is variation and thereby evolution dependent on external conditions?

After long and ingenious speculative discussions during the last four decades of the nineteenth century, in which the names of NÄGELI, WEISMANN and HAECKEL were prominent, attempts were made by means of experiments to obtain the answer which did not become evident from the discussion.

The first to take this decisive step was DARWIN's own cousin, FRANCIS GALTON, the famous statistician and eugenicist. GALTON argued that if DARWIN's theory was correct it would be possible to catch the pangenes carried by the blood stream and transfer them to another individual. He therefore carried out some experiments by transfusing blood, for instance, from a black rabbit to a white one. This white rabbit was then mated with an untreated white rabbit. It should be expected that the offspring would be black or mottled. This was not the case however. The offspring was white, and from this GALTON concluded that DARWIN's pangenesis theory was not true. Even if this experiment is not conclusive it is of great interest as being the first noteworthy attempt to solve the problem of variation on experimental lines.

But the one who first led the study of the origin of species into new paths by subjecting it to experiments on a large scale was the Dutch plant-physiologist HUGO DE VRIES. No one had previously thought that this was possible. Evolution was regarded as a historical process, advancing so slowly onwards that we were unable to follow its revolutionary effect, as our lives do not last long enough. As an illustration of this point of view we may cite the words of LAMARCK:

»If we lived for a still shorter time, for instance, for one second, then even the minute hand of a watch would be thought to stand still, and not even the accumulated observations of 60 generations would convince us that it moved». It was therefore quite natural that proofs of the evolutionary process *must* be sought for in the *historical evidence* found in the structure and distribution of the organisms and in their succession in the geological deposits. HUGO DE VRIES demonstrated that the phenomenon of the origin of species was something that was taking place also *in the present*, before our eyes.

The starting-point of his experiments were the statements found in the literature that certain widely different varieties had arisen quite suddenly from the parent species. Even DARWIN, who held the opinion that new varieties differed only gradually and slightly from the originative species, mentions certain varieties of this kind, which he called single variations.

HUGO DE VRIES therefore introduced into the Botanical Gardens in Amsterdam several species of plants which he cultivated in great individual numbers with a view to demonstrate experimentally this new-formation of species. In one instance the results also fulfilled his expectations, viz. the large-flowered evening primrose, *Oenothera Lamarckiana*. From the stock species there appeared among cultures of several 100,000 plants a score or so of new variation forms. They occurred quite suddenly, were widely different in all their organs and parts, were not connected to the parent species by intermediate forms and were at once cut and dried, constant. They were all at once new species that had advanced by leaps, mutations, as he called them. In type they were quite different from one another. One had gigantic flowers, one was a dwarf, one had large pale buds, but the stem was so slender that the top hung down. One had a red stem and red buds and such brittle branches that they broke off like glass-rods if they were touched brusquely. The variations thus took place in all directions, without plan or method. The cause could *not be due to the environment*, for all these extremely different varieties appeared under *exactly the same conditions* in DE VRIES' experimental garden. They could thus not be a manifestation of the transmission of acquired characters. And indeed, HUGO DE VRIES also denied the possibility of such a transmission of characters. In his opinion the origin of species did not take place by means of a slow process of adaptation, but advanced by leaps, by mutations, by means of an internal process, a re-arrangement of the hereditary substance.

HUGO DE VRIES' mutation theory seemed to furnish strong evidence in favour of DARWIN's original theory of natural selection. It even removed some of the difficulties of this theory. DARWIN had imagined that evolution progressed gradually and continuously by a series of minute steps of variation. The objection had been made that an evolution extending from amoeba to man under such circumstances would take such immeasurable ages that the geological age of the earth did not suffice. These variations by way of »lifts» or »leaps» changed the whole situation. And as a typical example of the optimism with which DE VRIES and many others with him at the beginning of this century regarded the evolutionary theory I may mention his computation of the necessary number of mutation steps or links in the evolutionary chain. He had discovered that of all the species he had examined *Oenothera Lamarckiana* alone was mutable. From this he concluded that this species was in a period of mutation, the others were not. Mutation was confined to certain periods, between which there occurred periods of quiescence. What was then the period of time elapsing between two successive waves of mutation? In the old Egyptian pyramid tombs fragments of plants had been discovered which proved to be representatives of species of plants still growing in that region. Thus, these plants had not changed for about 4000 years. This figure was taken by DE VRIES as the minimum value of a mutational interval. Then the only thing necessary was to know the time of the existence of life on the earth. According to the calculations of Lord KELVIN this was estimated at 24 million years (at present this figure is considered to be much higher). A simple division then gave the number of mutational periods at 6000. The entire process of evolution was therefore explained by 6000 mutational waves, according to DE VRIES!

But this new blossoming of the evolutionary theory did not last for many years. For along with his bosom child, the mutation theory, DE VRIES was also nursing a foster-child, Mendelism, and it was the foster-child that developed the more rapidly. DE VRIES was one of those who rescued MENDEL's discoveries from oblivion. And these discoveries gave *quite a new aspect* to the problem of the origin of species. For they taught us that the individual is constituted of hereditary units, or as they have since been called, genes, which are as supreme and as unchangeable as the atoms of chemistry. And from this it follows that *if two individuals have different hereditary units*

*these genes cannot fuse into a new gene in the offspring, any more than two different atoms can fuse into a new atom.*

Thus, if two different varieties are crossed there takes place in the offspring instead a re-combination, a re-organization of their free and independent genes so that new varieties are produced. Children become unlike their parents because the separate characters or genes of the latter are re-grouped in new ways in the different children. And the *number of varieties* produced in this way is a *pure function* of the *number of distinguishing characters* in the parents. If the parents differ in two characters only two new varieties can be formed. But if they differ in 10 characters not less than 1022 new varieties would be formed, all differing in some character from the parents, while if they differ in 20 characters the number of new varieties produced would be well over a million. *The greatness of MENDEL's discovery is that it has settled the apparently unsolvable conflict between heredity and variation, the preservative and the creative factor in the origin of species.* On what does heredity depend? It depends on the transmission of a certain hereditary unit, a certain gene, to the offspring. On what does variation depend? It depends on the re-grouping of the different genes of the father and mother.

Mendelism introduces us into an entirely new world of conception. The forms of variability that DARWIN and all others after him *imagined as successively emerging from one another along the ages like variation chains*, need not be so. They can in a single moment be created from one and the same cross by the thousands and the millions, as a great *sphere of variants*. They can often be *classified* in accordance to their appearance into series of variations, but they have *not appeared* in that series. We classify everything according to likeness, but likeness does not therefore prove for certain any *evolutionary* likeness, only a *constitutional* likeness.

Mendelism has thus solved the problem of variation and also solved the problem of heredity, but at the same time its results on the theory of evolution are similar to the result of a boulder falling into a narrow stream. For the main result of MENDEL's discovery is this: *Genes are constant*. They are not influenced either by one another or by the environment. Variation is caused by the re-combination of the genes, not by their change. Variation is therefore restricted by the combination possibilities of the genes. And these are limited by the crossing possibilities. Then again, since individuals belonging to different species of plant or animal cannot even be paired, much less produce offspring,

the combination of variations is confined to the species. Variants are formed, out-crossed and arise anew in a kaleidoscopic sequence *within* the species. *But the species remains the same sphere of variation.* The various species will remain like circles that do not intersect. *Species are constant.*

With the solution of the conflict between variation and heredity a new conflict has arisen, that between Mendelism and evolution. Is this conflict then a serious one?

So far, we have not at any rate reached exactly any critical point. A remaining possibility is that new hereditary units, new genes, may be formed. And how can this come about? By mutation. We must therefore return to this phenomenon of variation and review the results of research since the days of DE VRIES.

*Oenothera Lamarckiana* is by no means the only known mutating species. In numerous plants and animals suddenly arising varieties have been discovered. Mutation affects the most widely different characters. But the change is certainly not always so great as in *Oenothera*, often it is very slight. Thus, for instance, in the common black-oats there occur plants in which only the colour of the grains is changed into white. But in other cases there arise plants the whole appearance of which resemble the wild oat-grass, *Avena fatua*, thus, they are very greatly modified. Occasionally the change may effect not only the external appearance of the plant but also its entire natural metabolism. An American researcher, EYSTER, found a singular mutation in maize, which was pale-green in colour and stunted in size. A remarkable feature in this mutant was that it continually exuded drops of fluid at the tips of its leaves, and still more remarkable was that these leaves were much frequented by flies. He therefore analysed this fluid and found that it was made up of a dextrose solution. The plant did not possess the ability to convert the sugar formed into cell-tissue for its growth. The mutated character was that it had got diabetes. And indeed it also died from diabetes after a month or so. In this case the mutation was of a disastrous nature. In the same manner mutants have been found to occur in several species of plants which lack the power of producing the green chlorophyll. They become snow-white. But since chlorophyll is necessary in the preparation of their sustenance they die as soon as they have consumed the reserve nourishment they brought with them in the seed. In the cereals these chlorophyll deficient plants may live for a couple of weeks, in the horse-bean, which has especially large seeds, they may even reach

the flowering stage, but they never reach the seed-setting stage and therefore they never produce any offspring.

The occurrence of mutants has been observed not only in plants but also in animals. And the most talked of species at present and the one most closely studied with regard to its mutability is the little fruit fly, *Drosophila melanogaster*. It is T. H. MORGAN, who was last year awarded the Nobel Prize, and his indefatigable band of associates who have been carrying on an extensive and intensive research on heredity in this little insect. Since 1910, when the work began, over 20 million flies have been bred and examined. The result has also been magnificent, for over 400 mutants have been recorded. Even here the new character occasionally constitutes but a very slight change. In some instances single distinct bristles on the body are not developed, or they may be short while in others they are twisted, as if they were singed. Or the crimson colour of the eye may be changed and in extreme cases become pure white. But in between some 30 mutants are known, all of them indicating minute gradations of shade in the colour of the eyes from dark to pink, but all strictly hereditary. In other cases the shape and position of the wings are changed to such an extent that they are more or less useless and in extreme cases the wings disappear so that entirely wingless mutants are produced. Sometimes development is interfered with to such an extent that mutants occur with abnormally developed and twisted abdomens or with short and dachshous legs or with feet growing double. Even entirely sterile mutants occur, without any generative faculty. But the most remarkable occurrence is that sometimes the mutated character is a so-called lethal gene, which kills its possessor. When present this gene kills the new mutant, in certain cases already in the embryonic stage or larval stage, while in other cases the mutant reaches the pupal stage or even hatched imago. In the last-mentioned case sometimes boils or malign tumours grow all over the young grubs. In *Drosophila* about 60 genes are known, which are in this way deadly, lethal.

Mutations, that is, forms of variations, which do not appear possible of being classified in the ordinary Mendelian scheme of variations thus occur. They are said to arise spontaneously by a sudden gene change or by a change in the gene-bearing elements — the chromosomes — in the nucleus of the cell. Here we then have an entirely new regenerative factor with respect to variations. Here we have *new possibilities of evolution*.

But — and there is really another but — it is *not enough* that



mutations are *formed*. We must be quite certain that they are *caused by gene changes*, and that the change is in a positive, in an *evolutionary direction*.

That the mutations in certain cases are not due to gene changes has been conclusively proved by recent researches. And they arise in an entirely unexpected and quite fantastic manner. It has been found that certain varieties are, we are tempted to say, a kind of double entities. They have also been called *chimaeras*. Such varieties are found among our common pelargonium. They are recognized by their mottled leaves. If we make an anatomical examination of a plant having white margined leaves we shall see that the outer cell layer or layers are made up of white cells but underneath there are green tissues. The entire plant is like a green frame-work covered with a white mantle. These varieties have therefore been called *periclinal chimaeras*.

It now happens that in certain cases branches with purely green leaves appear on these white-margined plants. It was formerly thought that a mutation, and in this case a bud mutation, had taken place. But now that we know the nature of the plant the process gets quite a different explanation. The bud is produced in the green inner tissue. But in growing it does not as usual push the white mantle before it and thus become enveloped in it but instead it perforates the mantle. The shoot will be built up entirely of green tissue.

When the chimaera is composed of two differently coloured and thus easily discernible layers, as in the case just mentioned, it is not difficult to discover. But in other cases, where the character concerned is manifested only in a part of the plant the matter is considerably more difficult. But if the mantle is thick and the frame-work situated so deep down that the *gemmae* are produced entirely in the mantle then the chimaerical nature of the plant remains hidden unless some incidental damage causes an origin of the buds deeper in the tissue than usual. That such hidden chimaeras, *cryptochimaeras*, are really found has been shown during the last few years by means of purely experimental investigations. And *variation forms have been produced which were formerly known only as rarely occurring mutants*. A Russian lady, T. ASSEYEVA, has by extracting the eyes of a potato produced new buds deeper in the tuber than usual. From a common sort of potato, »Wohltmann», which has red tubers, she obtained by this means a variety having white tubers. This was known formerly as a spontaneous mutant. By the same method she succeeded later on in

producing quite a number of new varieties, some of them previously known as mutants. A Dutch investigator, DE MOL, has by injuring the inner tissues of hyacinth bulbs also produced a number of new varieties, which were also known previously as mutants. He was able to obtain the same result by X-ray radiation, as this likewise caused disturbance in the tissue.

Now the objection might be made that in all these cases entire shoots were changed. But in mutation it is only the germ-cells, the sex-cells, that mutate as a rule, and that is quite a different matter. No, it is not. For the flower, too, is a shoot, and if this very shoot is perforated then the sex-cells formed in it will also be entirely or partially changed.

A great sensation has been caused in recent years by the experiments made by the American scientist MULLER in which he evoked mutation in *Drosophila* by means of X-ray radiation. Chimaeras (mosaics) are also known in *Drosophila*, indeed they are not rare, and it is quite probable that in this case radiation only caused disturbances in the tissue, by means of which hidden chimaerical constituents were differentiated in the same manner as in the case of the hyacinth mentioned above. That the mutational process is in general caused by a natural radiation is out of the question, as this does not amount to the quantitative values required to evoke mutants experimentally. *What part of the known mutants is caused by a real gene change and what part is caused by a chimaerical differentiation is at present impossible to say.* But if we assume that at any rate some of them are spontaneous gene mutations there still remains a few questions that call for an answer, viz. whether they run in a positive direction and whether they have an evolutionary selective value.

As regards the first question it is a remarkable fact that the *vast majority* of mutants have *not acquired* any new character by mutation but have instead *lost* one of the genes of the species. They are loss mutants. To build an evolution on such mutants it would be necessary to assume that a higher differentiation, a development, is associated with a loss of genes. The consequence of this would be that amoeba must be endowed with an enormously greater stock of genes than Homo, and no one will readily take the consequence of such a view. For then vertebrates would be in genetic equipment only greatly thinned amoebae.

A very *small number* of mutants seem, however, to have been enriched with a gene, to be positive new-formations, *progressive* mutants.

And for them the final test will therefore be of vital importance, and that is: Have they also a selective value, which enables them not only to prevail in the struggle for existence but also to oust the parent species?

As far as viability is concerned mutants are in general poorly equipped. Not less than 60 of the 400 mutants of *Drosophila* have obtained the new character to perish. Chlorophyll deficient and diabetic plants and flies with useless wings or cleft legs are also of course doomed to a rapid elimination. But even the less divergent mutants have a weaker constitution and a shorter duration of life than the parent species. This is clearly and conclusively shown by the fact that *mutants of Oenothera and Drosophila are not found in nature*. They occur of course also here and may quite casually be met with, but they are soon eliminated and do not form a component of nature's stock in trade, and much less are they able to oust the parent species. *They appear quite simply to be non-viable variants, which we may see only under certain favourable conditions of culture, but which in nature are quickly swept away and disappear without leaving any trace*. And this is true of the dominant mutants as well as of the loss mutants. As a rule it may be said that *the more divergent a mutant is the less viable it is*. To endeavour to build an evolution on mutants is more than difficult. It is like setting out on a stormy sea in a nutshell.

It is obvious that the investigations of the last three decades into the problem of the origin of species have not been able to show that a variational material capable of competition in the struggle for existence is formed by mutation. Further, as it has also been impossible to demonstrate a progressive adaptation by means of the transmission of acquired characters (all the numerous experiments made have yielded negative results), we are forced to this conclusion that *the theory of evolution has not been verified by experimental investigations of the origin of species*.

There is, I think, at present as little inclination to give ear to this result as there was seventy years ago to the conception of organic evolution. It is declared to be quite simply unreasonable and also perhaps immaterial. The theory of evolution has been adequately, and more than adequately, proved in its historical form, it is said. But are we so sure that what rises before our eyes, but has not been proved to grow, has really once had an exuberant power of growth? Are we quite certain that evolution is a natural process like the growth of an

organism from seed to a many-branched and blossoming tree? May it not be so that evolution is a stately edifice that we ourselves have erected, laid stone on stone and is now completed — and like every other building, dead. It is perhaps not a process that has been going on and is still going on in nature. This is a question that we shall be compelled to take up, whether we will or not. The situation demands it. For as scientists we cannot rest content with a *credo, quia absurdum*.

But is then biology without evolution conceivable? In that branch of science which I myself now represent, systematics, is not here the evolutionary theory an indispensable corner-stone? Do we not classify everything according to relationship? Yes, that is how we express it. But we classify however only according to *likeness*, and we cannot maintain that likeness denotes more than a *constitutional likeness*, the presence of the same genes, *isogenesis*, as it may be correctly formulated. It is at any rate in accordance with isogenesis that we have always classified and will always classify our systematic series. In this respect nothing will be changed and here no danger threatens. If we call them evolutionary series it is perhaps only a — *sit venia verbo* — poetical periphrasis of the result of research.

For the theory of evolution is surely, if we think a little more deeply on the matter, nothing but the last remnant of our anthropocentric conception. When DARWIN pulled Man from his unique position into the evolutionary series he placed him at any rate at the head, and NIETZSCHE had Man followed by Superman. NIETZSCHE's Superman lies crushed by the Great War and DARWIN's Evolution has been proved to be lifeless, and probably, what is worse, to have been a fiction. What then is the trend of Biology? Are we moving towards a new »ignoramus« conception? Certainly not. *We are advancing to Biology as an exact science*. Just as affinity in Chemistry or Mineralogy need not be based on the assumption that the elements have evolved from one another, from hydrogen to uranium, there is no more need of our basing the related series of biology on an evolution from amoeba to Homo and so on. From this point of view Man, like every other biological species, will be a determined sphere of variation. This is a point that must be kept in sight also by the practical system-builders of human social life and human culture. And the burning social problem of the future will certainly be more concerned with stabilization than with evolution.

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# ZUR GENETIK VON PHASEOLUS VULGARIS

## XI. EINE MUTANTE MIT EINFACHEN BLÄTTERN UND IHRE VERERBUNGSWEISE

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(With a summary in English)

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ANGEREGT durch meine Ergebnisse der genetischen Untersuchung eines bei *Pisum* aufgefundenen Typus mit einfachen Blättern (LAMPRECHT 1933 b) sowie durch die Feststellung eines Typus mit gleichfalls einfachen Blättern bei *Phaseolus multiflorus* seitens D. RIESER (1924) wurde im Jahre 1932 eine grosse Anzahl von Bohnenpflanzen — etwa 50 Tausend — gleich nach Ausbildung der ersten nach den Primärblättern erscheinenden Blätter auf das eventuelle Vorkommen eines solchen Typus untersucht.

Meinem damaligen Assistenten, Herrn JENS ROLL-HANSEN, ist es gelungen eine Pflanze mit diesem Typus in einer Versuchsparzelle der Handelssorte Favorit zu entdecken. Favorit ist eine typische Buschbohne mit begrenztem Stammwachstum, grüner Stammfarbe, unverzweigter Infloreszenzachse mit gewöhnlich 2—3 Nodien, grünen Hülsen vom Schwertbohmentypus, weissen Blüten und weissen, platten Samen. Favorit ist eine schwedische, ziemlich frühe Sorte.

Die aufgefundene, abweichende Pflanze unterschied sich nun nicht nur mit Hinsicht auf die Gestaltung der Blätter von Favorit. So zeigten die Hülsen der abweichenden Pflanze nicht Schwertbohnen- sondern Brechbohmentypus. Sie waren ziemlich breit, bei eben erreichter voller Länge jedoch bei unentwickelten Samen mit elliptischem Querschnitt (anstatt wie bei Schwertbohnen mit plattem) sowie unbedeutend gekrümmt. Die weissen Samen waren weniger platt als bei Favorit. Die Genenformel für die Testafarbe der Samen war  $pp\ cc\ JJ\ GG\ BB\ vv$ , was weiter unten bei der Analyse einer Kreuzung mit der abweichenden Pflanze als einem Elter bewiesen wird. Hier verdient erwähnt zu werden, dass einer meiner Linien aus der Sorte Favorit (Linie 28) die Genenformel  $pp\ cc\ JJ\ gg\ BB\ vv$  zukommt, was von mir in mehreren Kreuzungen bewiesen worden ist. Vergleiche LAMPRECHT 1932 c, Kreuzung Nr. 5 und Nr. 14 sowie LAMPRECHT 1933 a, Kreuzung Nr. 10.

Die abweichende Pflanze reifte ungefähr eine Woche später als Favorit. Übereinstimmung bestand in bezug auf Art des Wuchses, Stammverzweigung, Bau der Infloreszenzen, Hülsenfarbe, Farbe und Form der Blüten sowie Farbe der Samen.

Die abweichende Pflanze zeigte demnach gegenüber Favorit, soweit festgestellt werden konnte, Unterschiede in wenigstens fünferlei Hinsichten, nämlich: Form der Hülsen, Form der Samen, genotypische Konstitution für Testafarbe, Form der Blätter sowie schliesslich Zeitpunkt der Reife. In der Sorte Favorit konnte in meinem Material bisher keine Ausspaltung von Pflanzen beobachtet werden, die in einer oder mehrerer der eben genannten Hinsichten abgewichen wären.

Besonders hervorgehoben soll auch werden, dass die abweichende Pflanze in drei der genannten Eigenschaften, nämlich Form der Hülsen und Samen sowie Testafarbe (genotypische Konstitution) gegenüber Favorit dominant ist. Hinsichtlich der Formel für Testafarbe besteht allerdings auch die Möglichkeit, dass in Favorit hierfür zwei verschiedene Konstitutionen vorkommen. Beiden vorhin erwähnten Formeln entspricht ja reinweisse Testafarbe. Die Samenpartie der Sorte Favorit, in der die abweichende Pflanze aufgetreten ist, stammt von einer Vermehrung in Ungarn. Unter Hinweis auf das eben Angeführte erscheint es kaum möglich irgend etwas Sicheres über den Ursprung der in Rede stehenden Form anzugeben. Vielleicht hat sie mit der Sorte Favorit überhaupt nichts zu tun! Nur soviel dürfte sicher sein, dass sie mit Hinsicht auf die Blattform als Mutation anzusprechen ist.

Die Fertilität der in Rede stehenden Form scheint vollkommen normal zu sein. In den beiden Jahren 1933 und 1934 wurde sie vermehrt; 1934 verfügte ich über einen Bestand von etwa 250 Pflanzen, die bei okulärer Besichtigung in allen Eigenschaften Übereinstimmung zu zeigen schienen. Nur in bezug auf den Zeitpunkt der Reife schien der Bestand nicht ganz einheitlich zu sein.

Die Form der Blätter der Mutante geht am deutlichsten aus den Bildern in Fig. 1 und 2 hervor. In Fig. 1 sind zwei Teile ein und derselben Pflanze abgebildet. Aus diesen ist ersichtlich, dass die Pflanze sowohl einfache, ungeteilte wie auch zwei- und dreiteilige Blätter trägt. Wegen der einfachen Blätter soll diese Form als *unifoliata*-Typus bezeichnet werden. Die ungeteilten Blätter sind stets beträchtlich grösser als die Blättchen des gewöhnlichen dreiteiligen Bohnenblattes. Zum Vergleich sind in Fig. 3 einige Typen normaler Bohnenblätter, im gleichen Massstabe wie Fig. 1 und 2 verkleinert, abgebildet.

Die Blätter des *unifoliata*-Typus, ob sie nun ungeteilt, zwei- oder

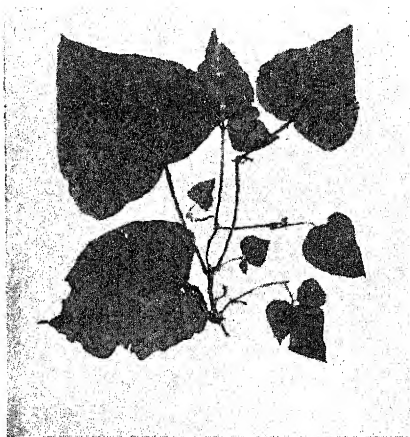


Fig. 1. Teile einer *Phaseolus*-Pflanze mit einfachen (*uni—uni*-) Blättern.

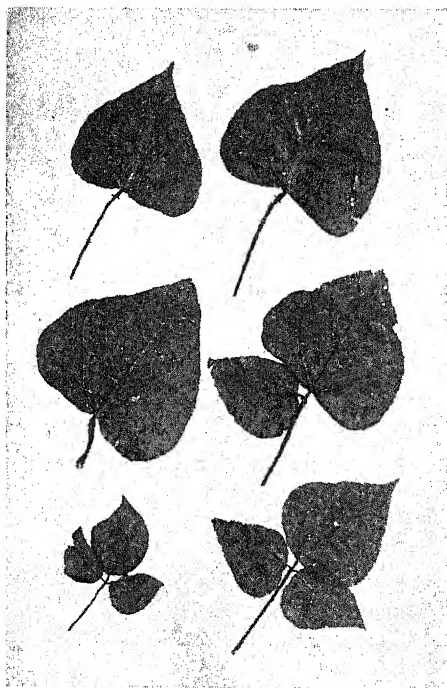
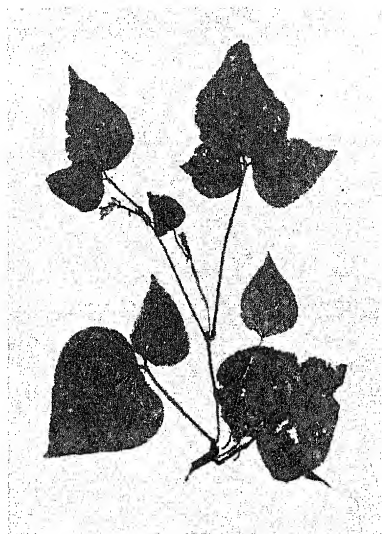


Fig. 2. Die verschiedenen bei *unifoliata*-Pflanzen auftretenden Blattypen.

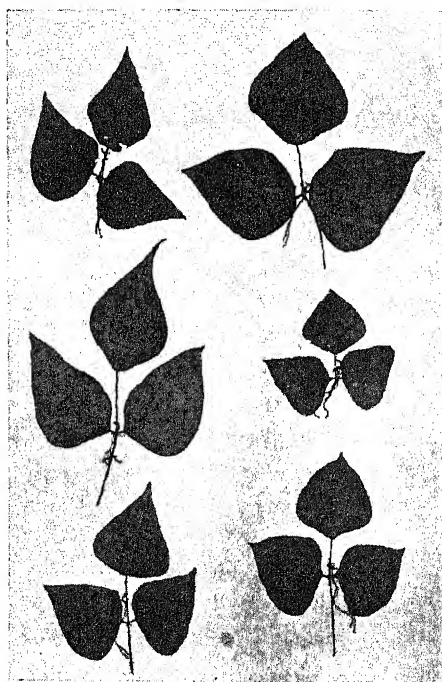


Fig. 3. Verschiedene Typen normaler, dreiteiliger Blätter von *Phaseolus vulgaris*.

dreiteilig sind, unterscheiden sich in mehr als einer Hinsicht scharf vom gewöhnlichen dreiteiligen Bohnenblatt. Was zuerst die Form der Blättchen vom *unifoliata*-Typus betrifft, so ist ihr Blattgrund gerade quer bis schwach herzförmig. Beim normalen Bohnenblatt ist der Blattgrund dagegen mehr oder weniger stark verschmälert, niemals herzförmig (vgl. die Figuren 1—3). Einen zweiten, durchweg typischen Unterschied findet man in bezug auf die Stipellen. Diese sind bekanntlich die kleinen, gewöhnlich lanzettlichen Nebenblätter der Teilblätter eines Blattes. Sie kommen namentlich in der Familie *Leguminosae* vor. In Fig. 4 ist links ein dreiteiliges Blatt einer *unifoliata*-Pflanze, rechts ein solches einer normalen Pflanze abgebildet.

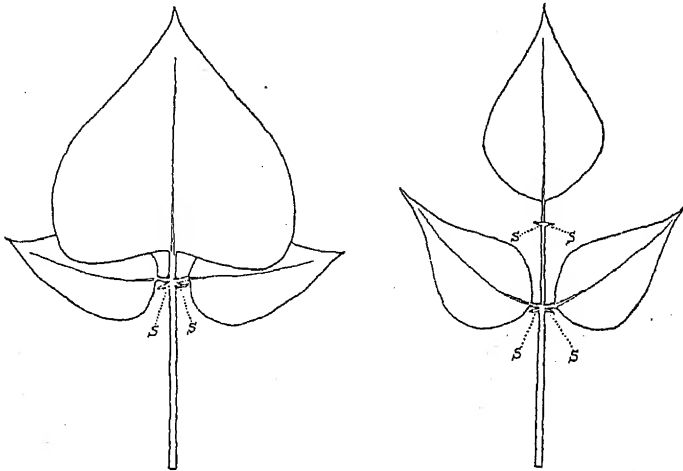


Fig. 4. Links dreiteiliges Blatt einer *unifoliata*-Pflanze, rechts dreiteiliges Blatt vom Normaltypus. s = Stipellen. (Etwas schematisiert.)

Aus Fig. 4 geht hervor, dass das gewöhnliche Bohnenblatt ein Stück ( $\frac{1}{2}$ —1 cm) unter dem Terminalblättchen ein Paar Stipellen, sowie unmittelbar unterhalb der beiden seitlichen Blättchen gleichfalls ein Paar solcher trägt. Die Blätter des *unifoliata*-Typus tragen dagegen immer nur ein Paar Stipellen, nämlich das obere kurz unter dem Terminalblättchen, und zwar gleichgültig ob ausser diesem noch ein oder zwei seitliche Blättchen vorkommen. In den letzten beiden Fällen entspringen die Blättchen nämlich ganz unmittelbar oberhalb dieser Stipellen und nicht an der bedeutend weiter unten am Blattstiel gelegenen Stelle, wo beim gewöhnlichen Blatt die seitlichen Blättchen ihren Ursprung haben und wo auch das untere Paar Stipellen solchenfalls sitzt.



Die Blätter des *unifoliata*-Typus unterscheiden sich demnach von jenen des Normaltypus in dreierlei Hinsichten: 1) Der Blattgrund der Blättchen ist gerade quer oder schwach herzförmig, statt mehr oder weniger verschmälert, 2) der Blattstiel trägt nur das eine Paar Stipellen kurz unter dem Terminalblättchen — das zweite, beim Normaltypus unmittelbar unter den Seitenblättchen sitzende fehlt, und 3) eventuell auftretende Seitenblättchen entspringen unmittelbar oberhalb des vorhandenen Stipellenpaares und nicht dort wo die Seitenblättchen des Normaltypus sitzen.

Das Auftreten eventueller seitlicher Blättchen an den Blättern des *unifoliata*-Typus unmittelbar oberhalb der Stipellen des Terminalblattes dürfte mit Hinsicht auf die morphologische Auffassung der letzteren ein gewisses Interesse besitzen. GOEBEL (1898—1901, 1923) schreibt über die Stipellen der *Leguminosae* folgendes: »Die Stipellen, die sich bei *Phaseolus*-, *Robinia*-, *Desmodium*-Arten und anderen Leguminosen an der Basis der Teilblättchen finden, sind dagegen offenbar rudimentäre Fiederblättchen, sie treten meist in Gestalt kleiner Zähne auf, sind aber gelegentlich z. B. bei *Robinia* an Stockausschlägen und anderen besonders kräftig ernährten Sprossen auch als Blättchen entwickelt. Dass es sich dabei um reduzierte Organe handelt, ist wahrscheinlich».

VELENOVSKÝ (1910) kann diese Auffassung GOEBELS nicht gutheissen, sondern kritisiert sie folgendermassen: »GOEBEL hat allerdings darin recht, dass sich bei den Leguminosen die Stipellen manchmal in flache Blättchen umwandeln, was man leicht an der gemeinen Akazie (Robinie) beobachten kann. Hieraus folgt aber durchaus nicht, dass die erwähnten Stipellen wahre Blätter sind, denn sie haben dieselbe Stellung und Gestalt wie die Nebenblätter am Hauptblattstiel. — Die Sache verhält sich jedoch anders, wenigstens darf sie nicht gleich verallgemeinert werden, wie es GOEBEL getan hat». VELENOVSKÝ (l. c.) berichtet dann über die Verhältnisse bei *Desmodium spirale* DC., bei welcher Art diese an ein und derselben Pflanze variieren. Am unteren Stammteil sitzen nur Blätter mit einem terminalen Blättchen, unter dem an der Basis eines gelenkigen Ansatzes ein Paar Stipellen entspringen — also genau wie bei den einfachen Blättern des *unifoliata*-Typus von *Phaseolus vulgaris*. Bei diesen Blättern kann es vorkommen, dass eine Stipelle in ein Blättchen umgewandelt erscheint. Die oberen Blätter sind bei *Desmodium* dreiteilig und tragen zwei Paare Stipellen. Diese haben dann genau gleiche Stellung wie beim gewöhnlichen dreiteiligen Blatt von *Phaseolus vulgaris* (siehe Fig. 4 rechts).

In bezug auf die gelegentliche Umbildung einer Stipelle in ein Blättchen bei *Desmodium* sagt VELENOVSKÝ: »Wenn sich also die Stipellen in flache Blättchen umändern, so bedeutet dies keine normale Blatteilung, da der ganze Plan der Blatteilung dieser Anschauung widerspricht. Es ist dies in der Tat eine zufällige, aber allerdings begreifliche Metamorphose, denn die Nebenblätter und Stipellen sind lediglich als ein Bestandteil des Blattes selbst anzusehen».

Der von mir vorhin beschriebene Blatttypus der *unifoliata*-Pflanzen von *Phaseolus vulgaris* bildet wohl eine weitere starke Bestätigung von VELENOVSKYS Auffassung der Stipellen. Beim *unifoliata*-Typus entspringen eventuelle seitliche Teilblättchen ganz unmittelbar im Anschluss an das Stipellenpaar, das ein Stück unter dem Terminalblättchen am Blattstiel sitzt. Mit Hinblick auf die Ursprungsstelle dieser seitlichen Blättchen erscheint die Auffassung der Stipellen als reduzierte Teilblättchen sinnwidrig. GOEBELS diesbezügliche Auffassung dürfte — wenigstens in bezug auf die Leguminosen — nicht aufrecht erhalten werden können. Die Stipellen dürften hier vielmehr mit Recht als wirkliche Nebenblätter der Teilblättchen anzusehen sein.

Zum Studium der Vererbungsweise des *unifoliata*-Typus wurden gleich im Jahre 1932 mit Pollen der Ursprungspflanze zwei Befruchtungen ausgeführt; die eine mit Linie 28, aus Favorit, der Sorte in der die Mutante angetroffen worden ist, die andere mit Linie 1, aus der schwedischen braunen Bohnensorte Stella. Die erste Kreuzung ist leider misslungen. Die zweite hat vier normal entwickelte Samen ergeben.

Linie 1 hat begrenztes Stammwachstum, rosa Stammfarbe, unverzweigte Infloreszenzachse mit in der Regel 2—3 Nodien, normale dreiteilige Blätter, grüne, gerade Hülsen mit elliptischem Querschnitt, laeliafarbige Blüten und Bister Testafarbe. Die Genenformel für die Testafarbe dieser Linie ist *PP CC JJ GG bb vv* (siehe LAMPRECHT 1932).

Die Pflanzen der ersten Generation dieser Kreuzung, Nr. 169, zeigten durchweg normale, dreiteilige Blätter, gleiche nur etwas längere Hülsen als Linie 1, rosa Stammfarbe und laeliafarbige Blüten. Die Samen zeigten die Testafarbe Mineralbraun/Rhamninbraun marmoriert.

Die normale dreiteilige Blattform dominierte demnach über den *unifoliata*-Typus, rosa über grüne Stammfarbe und laeliafarbige Blüten über weisse. Die gefundene Testafarbe war die theoretisch erwartete. Wie bereits früher erwähnt worden ist, kommt den Samen des *unifoliata*-Typus die genotypische Konstitution *pp cc JJ GG BB vv* zu. Die

$Uini$ $Pp$ $Cc$ $Bb$	$F_1$	$192$ $Uini$ (191,50)	$144$ $PP$ (143,10)	$36$ $CC$ (32,25)	$\left\{ \begin{array}{l} 27 \text{ } BB - \text{ gefunden: } 26,20 \\ 9 \text{ } bb - \text{ gefunden: } 6,05 \end{array} \right.$	$PP$ $CC$ $JJ$ $Gg$ $Bb$ $vv$ Bister
				$72$ $Cc$ (72,55)	$\left\{ \begin{array}{l} 54 \text{ } BB - \text{ gefunden: } 58,44 \\ 18 \text{ } bb - \text{ gefunden: } 14,11 \end{array} \right.$	$PP$ $CC$ $JJ$ $Gg$ $Bb$ $vv$ Mineralbraun/Rhaminbraun $PP$ $Cc$ $JJ$ $Gg$ $BB$ $vv$ Bister/Maisgelb $PP$ $Cc$ $JJ$ $Gg$ $bb$ $vv$ Rhaminbraun $PP$ $cc$ $JJ$ $Gg$ $BB$ $vv$ Maisgelb $PP$ $cc$ $JJ$ $Gg$ $bb$ $vv$ Reinweiss
				$48$ $PP$ (48,40)	$48 \dots$ — gefunden: 48,40	$pp$ mit sämtlichen Kombinationen der übrigen Gene Mineralbraun $PP$ $CC$ $JJ$ $Gg$ $BB$ $vv$ Bister $PP$ $CC$ $JJ$ $Gg$ $bb$ $vv$ Mineralbraun/Rhaminbraun $PP$ $Cc$ $JJ$ $Gg$ $BB$ $vv$ Bister/Maisgelb $PP$ $Cc$ $JJ$ $Gg$ $bb$ $vv$ Rhaminbraun $PP$ $cc$ $JJ$ $Gg$ $BB$ $vv$ Maisgelb $PP$ $cc$ $JJ$ $Gg$ $bb$ $vv$ Reinweiss
				$12$ $CC$ (4,04)	$\left\{ \begin{array}{l} 9 \text{ } BB - \text{ gefunden: } 4,04 \\ 3 \text{ } bb - \text{ gefunden: } 0 \end{array} \right.$	$pp$ mit sämtlichen Kombinationen der übrigen Gene Mineralbraun $PP$ $CC$ $JJ$ $Gg$ $BB$ $vv$ Bister $PP$ $CC$ $JJ$ $Gg$ $bb$ $vv$ Mineralbraun/Rhaminbraun $PP$ $Cc$ $JJ$ $Gg$ $BB$ $vv$ Bister/Maisgelb $PP$ $Cc$ $JJ$ $Gg$ $bb$ $vv$ Rhaminbraun $PP$ $cc$ $JJ$ $Gg$ $BB$ $vv$ Maisgelb $PP$ $cc$ $JJ$ $Gg$ $bb$ $vv$ Reinweiss
$Uini$ $Pp$ $Cc$ $Bb$	$F_1$	$64$ $uini$ (64,50)	$48$ $PP$ (48,33)	$24$ $Cc$ (30,23)	$\left\{ \begin{array}{l} 18 \text{ } BB - \text{ gefunden: } 22,16 \\ 6 \text{ } bb - \text{ gefunden: } 8,07 \end{array} \right.$	$PP$ $CC$ $JJ$ $Gg$ $Bb$ $vv$ Mineralbraun/Rhaminbraun $PP$ $Cc$ $JJ$ $Gg$ $BB$ $vv$ Bister/Maisgelb $PP$ $Cc$ $JJ$ $Gg$ $bb$ $vv$ Rhaminbraun $PP$ $cc$ $JJ$ $Gg$ $BB$ $vv$ Maisgelb $PP$ $cc$ $JJ$ $Gg$ $bb$ $vv$ Reinweiss
				$12$ $cc$ (14,11)	$\left\{ \begin{array}{l} 9 \text{ } BB - \text{ gefunden: } 12,09 \\ 3 \text{ } bb - \text{ gefunden: } 2,02 \end{array} \right.$	$pp$ mit sämtlichen Kombinationen der übrigen Gene Mineralbraun $PP$ $CC$ $JJ$ $Gg$ $BB$ $vv$ Bister $PP$ $CC$ $JJ$ $Gg$ $bb$ $vv$ Mineralbraun/Rhaminbraun $PP$ $Cc$ $JJ$ $Gg$ $BB$ $vv$ Bister/Maisgelb $PP$ $Cc$ $JJ$ $Gg$ $bb$ $vv$ Rhaminbraun $PP$ $cc$ $JJ$ $Gg$ $BB$ $vv$ Maisgelb $PP$ $cc$ $JJ$ $Gg$ $bb$ $vv$ Reinweiss
				$16$ $pp$ (16,12)	$16 \dots$ — gefunden: 16,12	$pp$ mit sämtlichen Kombinationen der übrigen Gene Mineralbraun $PP$ $CC$ $JJ$ $Gg$ $BB$ $vv$ Bister $PP$ $CC$ $JJ$ $Gg$ $bb$ $vv$ Mineralbraun/Rhaminbraun $PP$ $Cc$ $JJ$ $Gg$ $BB$ $vv$ Bister/Maisgelb $PP$ $Cc$ $JJ$ $Gg$ $bb$ $vv$ Rhaminbraun $PP$ $cc$ $JJ$ $Gg$ $BB$ $vv$ Maisgelb $PP$ $cc$ $JJ$ $Gg$ $bb$ $vv$ Reinweiss
				$16$ $pp$ (16,12)	$16 \dots$ — gefunden: 16,12	$pp$ mit sämtlichen Kombinationen der übrigen Gene Mineralbraun $PP$ $CC$ $JJ$ $Gg$ $BB$ $vv$ Bister $PP$ $CC$ $JJ$ $Gg$ $bb$ $vv$ Mineralbraun/Rhaminbraun $PP$ $Cc$ $JJ$ $Gg$ $BB$ $vv$ Bister/Maisgelb $PP$ $Cc$ $JJ$ $Gg$ $bb$ $vv$ Rhaminbraun $PP$ $cc$ $JJ$ $Gg$ $BB$ $vv$ Maisgelb $PP$ $cc$ $JJ$ $Gg$ $bb$ $vv$ Reinweiss

Schematische Darstellung der Aufspaltung des Bastarden  $Uini$   $Pp$   $Cc$   $JJ$   $Gg$   $Bb$   $vv$  in  $F_2$  der Kreuzung 169.  
Die in Klammern und vor den Farbnamen mitgeteilten Zahlen entsprechen den tatsächlich erhaltenen, umgerechnet auf die Kombinationszahl 256.

Samen der ersten Generation sollen daher die Konstitution  $Pp Cc Jj GG Bb vv$  haben. Da sie in bezug auf das Gen  $C$  heterozygot sind, soll die Testa marmoriert sein, was auch eingetroffen ist. Der angeführten Formel entspricht die Testafarbe Mineralbraun/Rhamninbraun heterozygot marmoriert. In bezug auf die Bezeichnung der in vorliegender Kreuzung ausspaltenden Testafarben und die diesen entsprechenden Genenformeln verweise ich auf meine früheren diesbezüglichen Arbeiten (LAMPRECHT 1932 a, 1932 b, 1932 c und 1933 a), in denen alle diese eingehend beschrieben sind.

Die zweite Generation bestand aus 127 Pflanzen, die in bezug auf alle in Frage kommenden Eigenschaften beurteilt werden konnten. Im ganzen wurden 150 Samen ausgesät, aus denen sich 143 Keimpflanzen entwickelt hatten. Von diesen sind 16 in verschiedenen Entwicklungsstadien zugrunde gegangen oder haben keine Samen ergeben. Es konnten also nur 127 Pflanzen, das sind 84,8 %, zur genischen Analyse verwendet werden.

Das Eigenschaftspaar normale dreiteilige Blätter — *unifoliata*-Blätter zeigte monohybride Spaltung. Das diesem Eigenschaftspaar zugrunde liegende Genpaar soll, abgeleitet von der rezessiven Eigenschaft *unifoliata*, mit *Uni—uni* bezeichnet werden. Für die in Frage stehende Spaltung resultierten folgende Zahlen:

Gefunden: 95 *Uni* : 32 *uni*

Erwartet: 95,25 » : 31,75 »

D/m für 3 : 1 = 0,05

Die Zahlen zeigen geradezu ideale monohybride Spaltung an.

Für das Genpaar  $P—p$ , Anwesenheit von  $P$  ist Bedingung für die Ausbildung von u. a. Testafarbe, wurde genau dieselbe Spaltung wie für *Uni—uni* gefunden, nämlich 95  $P$  : 32  $p$  mit D/m für 3 : 1 = 0,05. Erwähnt sei hier auch, dass sämtliche Pflanzen mit  $pp$  reinweisse Blüten und grüne Stammfarbe zeigten. Anwesenheit von  $P$  scheint demnach auch für die Ausbildung von Blütenfarbe und rosa Stammfarbe Bedingung zu sein.

Die für die Spaltung in den vier Genpaaren *Uni—uni*,  $P—p$ ,  $C—c$  und  $B—b$  erhaltenen Zahlen sind in der schematischen Darstellung auf Seite 244, umgerechnet auf die Kombinationszahl 256 wiedergegeben. Die entsprechenden Zahlen sind dort in Klammern bzw. vor den Farbnamen angeführt. Wie aus diesen ersichtlich ist, besteht durchweg befriedigende Übereinstimmung mit den theoretisch erwarteten Werten.

Dasselbe ergibt sich auch aus den unten mitgeteilten bifaktoriellen Spaltungsverhältnissen.

Für die Spaltung hinsichtlich *Uni—uni* und *P—p* resultierte:

Gefunden: 71 *Uni P* : 24 *Uni p* : 24 *uni P* : 8 *uni p*

Erwartet: 71,44 » : 23,81 » : 23,81 » : 7,94 »

D/m für

9 : 3 : 3 : 1 = — 0,08      + 0,04      + 0,04      + 0,02

Es besteht demnach ungewöhnlich gute Übereinstimmung mit den theoretisch erwarteten Spaltungszahlen. Wahrscheinlich besteht also unabhängige Vererbung zwischen *Uni* und *P*.

Für die Spaltung *Uni—uni* und *C—c* ergab sich:

Gefunden: 52 *Uni C* : 19 *Uni c* : 17 *uni C* : 7 *uni c*

Erwartet: 53,44 » : 17,81 » : 17,81 » : 5,94 »

D/m für

9 : 3 : 3 : 1 = — 0,30      + 0,31      — 0,20      + 0,45

Auch hier herrscht sehr gute Übereinstimmung zwischen dem theoretisch erwarteten und dem gefundenen Spaltungsverhältnis; und wahrscheinlich werden die in Rede stehenden beiden Genpaare unabhängig voneinander vererbt. Für die Klassifikation im Genpaar *C—c* gleichwie auch im Genpaar *B—b* konnten natürlich nur die Individuen mit *P*, nämlich 95 mit gefärbter Testa, in Frage kommen, und gilt hierfür als Bedingung für die Zulässigkeit einer solchen Berechnung unabhängige Vererbung der Genpaare *C—c* und *B—b* von *P—p* sowie Spaltung ohne Komplikationen, was hier der Fall zu sein scheint.

Für die Genpaare *Uni—uni* und *B—b* resultierte:

Gefunden: 56 *Uni B* : 15 *Uni b* : 19 *uni B* : 5 *uni b*

Erwartet: 53,44 » : 17,81 » : 17,81 » : 5,94 »

D/m für

9 : 3 : 3 : 1 = + 0,53      — 0,74      + 0,31      — 0,40

Auch hinsichtlich dieser beiden Genpaare besteht befriedigende Übereinstimmung zwischen dem theoretisch erwarteten und dem gefundenen Spaltungsverhältnis, und damit wahrscheinlich unabhängige Vererbung derselben.

Die übrigen in Kreuzung Nr. 169 festgestellten dihybriden Spaltungsverhältnisse werden unten kurz zahlenmässig angeführt. Aus den Spaltungszahlen geht hervor, dass auch die dort angeführten Genpaare wahrscheinlich unabhängig voneinander vererbt werden.

Gefunden: 69  $PC : 26$   $Pc : 32$   $p \begin{pmatrix} C \\ c \end{pmatrix}$

Erwartet: 71,44 » : 23,81 » : 31,75 »

D/m für

$$9 : 3 : 4 = -0,44 \quad +0,50 \quad +0,05$$

Gefunden: 75  $PB : 20$   $Pb : 32$   $p \begin{pmatrix} B \\ b \end{pmatrix}$

Erwartet: 71,44 » : 23,81 » : 31,75 »

D/m für

$$9 : 3 : 4 = +0,64 \quad -0,87 \quad +0,05$$

Gefunden: 55  $CB : 14$   $Cb : 20$   $cB : 6$   $cb$

Erwartet: 53,44 » : 17,81 » : 17,81 » : 5,94 »

D/m für

$$9 : 3 : 4 = +0,32 \quad -1,00 \quad +0,58 \quad +0,03$$

Wie vorstehend erwähnt worden ist und wie die Figuren 1 und 2 zeigen, tragen die *unifoliata*-Pflanzen sowohl einfache, ungeteilte wie auch zwei- und dreiteilige Blätter. Die gleiche Erscheinung ist von mir früher (LAMPRECHT 1933 b) für einen *unifoliata*-Typus von *Pisum* beschrieben und auf ihre Vererbung hin untersucht worden. Bei diesem hat sich gezeigt, dass die einfachen Blätter durchweg unten und oben am Stamm, aber nur selten und dann vereinzelt in der Mitte desselben auftreten. Ähnliches scheint auch für den *unifoliata*-Typus von *Phaseolus vulgaris* Gültigkeit zu haben. Auch hier findet man die einfachen Blätter hauptsächlich am Grunde und an der Spitze der Stammverzweigungen.

Bei *Phaseolus* kann natürlich die Auszählung der Blatttypen (einfache, 2- bzw. 3-teilige, bezeichnet mit 1, 2 und 3) wegen des abweichenden Verzweigungstypus nicht in gleicher Weise wie für *Pisum* stattfinden, wo die Blätter am Hauptstamm von unten nach oben der Reihe nach angegeben werden können. Für einen Vergleich des allgemeinen Typus und der Frequenz von einfachen, 2- bzw. 3-teiligen Blättern kann jedoch einfach die Anzahl solcher per Pflanze angegeben werden. Als Beispiel führe ich hier die entsprechenden Zahlen für 10 *unifoliata*-Pflanzen von *Phaseolus* sowie Durchschnittswerte für aus zwei *Pisum*-Linien ausspaltende *unifoliata*-Pflanzen an.

In bezug auf die *uni—uni*-Pflanzen von *Pisum* sei erwähnt, dass sie im Gegensatz zu jenen von *Phaseolus vulgaris* steril sind; sie haben

wiederholt verzweigte Infloreszenzen und pistilloid umgebildete Blütenelemente; siehe LAMPRECHT 1933 b. Die aus der *Pisum*-Linie 187 ausspaltenden *uni—uni*-Pflanzen sind mit Hinsicht auf die Frequenz von einfachen, 2- bzw. 3-teiligen Blättern praktisch genommen konstant. Aus der *Pisum*-Kreuzung Nr. 59 ausspaltende *uni—uni*-Pflanzen zeigen jedoch eine beträchtliche Variation in dieser Hinsicht. Und Ähnliches scheint für die in der *Phaseolus*-Kreuzung Nr. 169 ausspaltenden *uni—uni*-Pflanzen zu gelten. Für die in der Tabelle aufgenommenen Pflanzen erhält man eine mittlere Frequenz für einfache Blätter von

*Tabelle über die Frequenz einfacher, 2- und 3-teiliger Blätter an unifoliata-Typen von Phaseolus vulgaris und Pisum sativum.*

Bezeichnung der <i>unifoliata</i> -Pflanzen	A n z a h l B l ä t t e r			
	einfach	2-teilig	3-teilig	Summe
<i>Phaseolus</i> Kr. 169, 4283/2	7	5	23	35
/26	9	2	11	22
/38	6	1	11	18
/39	8	1	10	19
/41	8	4	12	24
/44	15	7	13	35
/80	8	4	17	29
/87	18	6	5	29
/95	4	4	19	27
/97	18	10	10	38
<i>Pisum</i> aus L. 187	10	3	4	17
aus Kr. 59	6	3	8	17

36,5 %, für 2-teilige von 16 % und für 3-teilige von 47,5 %. Gewisse Pflanzen zeigen hiervon jedoch eine sehr starke Abweichung, und zwar in verschiedenen Richtungen. So hat Pflanze 4283/2 nicht weniger als 66 % 3-teilige Blätter, Pflanze 4283/87 dagegen nur 17 % solche. Offenbar gibt es verschiedene Typen von *uni—uni*-Pflanzen, deren Habitus noch durch andere Genpaare als durch *Uni—uni* bestimmt wird, ähnlich wie ich dies für die *uni—uni*-Pflanzen in der *Pisum*-Kreuzung Nr. 59 habe nachweisen können (LAMPRECHT 1933 b).

Sollte sich herausstellen, dass die von mir studierte *uni—uni*-Mutation von *Pisum sativum* eine Komplexmutation darstellt, was ich nunmehr für sehr wahrscheinlich halte — sodass also die wiederholte Verzweigung der Infloreszenz und die pistilloide Umbildung der Blütenelemente auf besondere Genpaare zurückzuführen wären — dann er-

scheint es auch sehr wahrscheinlich, dass wir es in *Pisum sativum* und in *Phaseolus vulgaris* mit homologen *Uni—uni*-Genpaaren zu tun haben.

### SUMMARY.

1. The author describes a mutation of *Phaseolus vulgaris* with simple, entire leaves — an *unifoliata* type — occurring in the Swedish variety of French bean, Favorit. This mutation differs however somewhat in several respects from Favorit, for instance, in the type of pod, the shape of the seeds and the genotypic constitution of the colour of the testa. For this reason nothing definite can be said of its origination.

2. In the *unifoliata* type there occur in addition to simple leaves also bipartite and tripartite leaves in varying frequency. The leaves however always differ from the normal tripartite bean-leaf in the following respects: 1) the base of the leaf is straight across to slightly cordate instead of tapering, 2) on the leaf-stalk there is only one pair of stipellae just below the terminal leaflet, and 3) possibly occurring lateral leaflets proceed from above and in immediate association with the pair of stipellae mentioned in 2) and not at the spot where lateral leaflets are situated in the normal type (cp. figs. 1—4).

3. The site of origin of any possibly occurring lateral leaflets — in immediate association with stipellae — argues, in the opinion of the author, against GOEBEL's view that they are to be regarded as reduced leaflets.

4. The character-pair, normal type — *unifoliata* type, of bean-leaves shows a monohybrid segregation. The causal pair of genes is designated by *Uni—uni* — derived from *unifoliata*.

5. In a cross, No. 169, an examination was made at the same time of the segregation in the gene-pairs *Uni—uni*, *P—p*, *C—c* and *B—b*. The segregation numbers obtained renders an independent inheritance of these four pairs of genes highly probable.

6. In conclusion the author calls attention to an analogous occurrence in *Pisum*, a *unifoliata* type, in which simple, bipartite and tripartite leaves occur. In both *Phaseolus vulgaris* and *Pisum sativum* it is possibly a question of two homologous pairs of genes.



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# CHROMOSOME BEHAVIOUR IN SOME NICOTIANA HYBRIDS

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SVALÖF, SWEDEN

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## INTRODUCTION.

THE cytological observations reported in the present paper were made during a stay at the College of Agriculture, University of California, Berkeley. In order to become more acquainted with the *Nicotiana* material grown by Prof. R. E. CLAUSEN I studied meiosis in some hybrids, which were generously left at my disposal by Prof. CLAUSEN. The observations made are rather incomplete, but as the results are in part somewhat unexpected they will be briefly reported as a contribution to the cytology of the genus.

Two different  $F_1$  hybrids were examined, *Nicotiana bonariensis* LEHM.  $\times$  *Langsdorfii* WEIMM. and *N. glutinosa* L.  $\times$  *tabacum* L. In connection with the latter hybrid some observations on the chromosome behaviour of the synthetic species »*N. digluta*» were also made. As is well known *N. digluta* arose from the cross *N. glutinosa*  $\times$  *tabacum* (CLAUSEN and GOODSPEED 1925) and represents one of the very first examples of allopolyploidy.

The meiotic observations were made on smear preparations of pollen mother cells from plants cultivated in a greenhouse. The smears were fixed in chromacetic formalin and stained with gentian violet. This method gave rather satisfactory results and the slides obtained in this way seem to be superior to ordinary acetocarmine preparations.

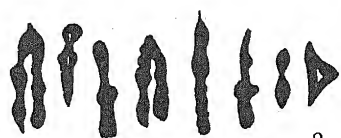
Before going into details I wish to express my sincere gratitude especially to Prof. CLAUSEN, Prof. E. B. BABCOCK, Dr. W. LAMMERTS and Dr. P. AVERY for generous supply of material, excellent working facilities and helpful discussions, and to Mrs. G. MÜNTZING for valuable technical assistance. My stay in Berkeley was made possible by grants from the Swedish—American Foundation and the Kungl. Hvitfeldtska Stipendieinrättningen.

## NICOTIANA BONARIENSIS $\times$ LANGSDORFII.

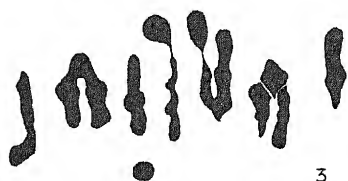
The hybrid *bonariensis*  $\times$  *Langsdorfii* flowered abundantly and had plenty of buds, but nevertheless it was found to be a less suitable



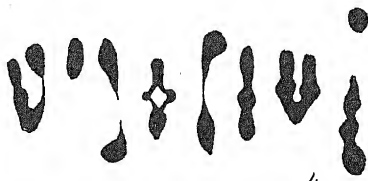
1



2



3



4



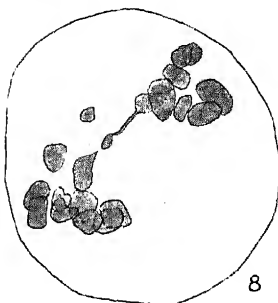
5



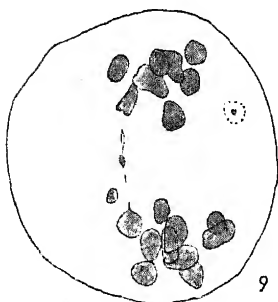
6



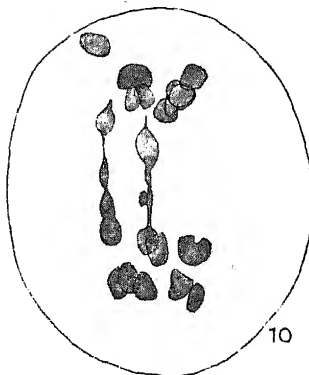
7



8



9



10

material for cytological studies than the other *Nicotiana* types examined. This was chiefly due to the fact that this hybrid had rather small anthers, which were difficult to smear. However, some rather good slides were obtained.

As the parent species have the same chromosome number ( $n=9$ ) and belong to the same group of the genus, the *alata* group (cf. GOODSPEED 1933), the  $F_1$  hybrid might be expected to form 9 bivalents or a variable number of bivalents and univalents. However, much to our surprise, first metaphase in the hybrids was characterized by a frequent occurrence of trivalents in addition to a variable number of bivalents and univalents. No clear associations of more than three chromosomes could be detected, but in one cell a probable quadrivalent was observed. Though consequently the occurrence of more compound associations than trivalents is not quite excluded, their frequency must be very low, compared to that of the trivalents. In 23 cells examined the number of trivalents ranged from one to four, the average value being 2.5. The number of cells with 0—4 trivalents was as follows:

Number of trivalents: .....	0	1	2	3	4
Number of cells: .....	0	3	8	10	2

In the same cells the number of bivalents and univalents could also be counted. The following complete configurations were found (table 1).

TABLE 1. *Chromosome configurations in N. bonariensis*  $\times$  *Langsdorfii*,  $F_1$ .

Configurations	Number of cells
$3_{III} + 4_{II} + 1_I$ .....	9
$2_{III} + 5_{II} + 2_I$ .....	4
$1_{III} + 7_{II} + 1_I$ .....	3
$2_{III} + 6_{II}$ .....	3
$4_{III} + 2_{II} + 2_I$ .....	1
$3_{III} + 3_{II} + 3_I$ .....	1
$4_{III} + 3_{II}$ .....	1
$1_{IV} + 2_{III} + 4_{II}$ .....	1(?)

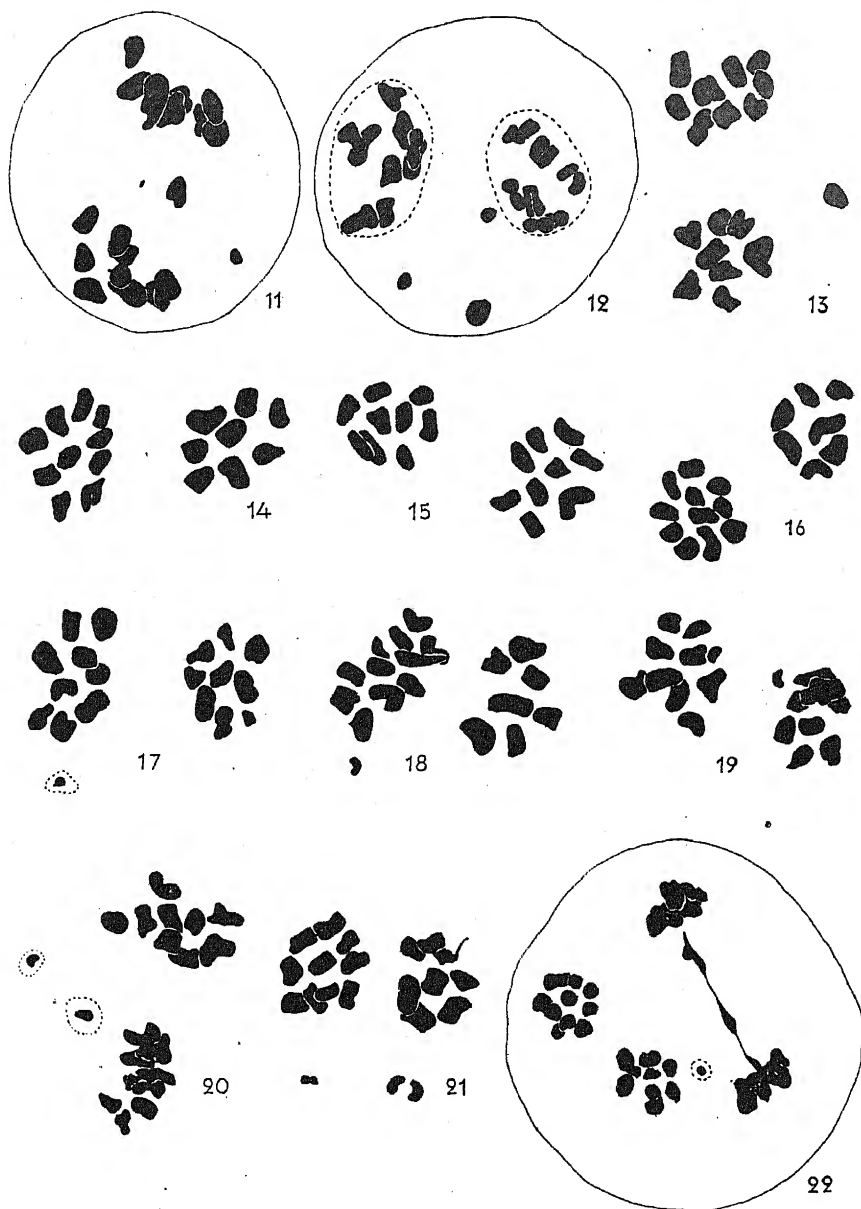
Figs. 1—10. Meiosis in *N. bonariensis*  $\times$  *Langsdorfii*,  $F_1$ . — Figs. 1—4, first metaphase, side view (separately drawn); fig. 1,  $2_{III} + 5_{II} + 2_I$ ; fig. 2,  $2_{III} + 6_{II}$ ; fig. 3,  $3_{III} + 4_{II} + 1_I$ ; fig. 4,  $2_{III} + 5_{II} + 2_I$ . — Figs. 5—6, first anaphase without complications; fig. 5, distribution 8—10; fig. 6, distribution 7—11. — Figs. 7—10, first anaphase with attenuated chromosomes and fragments; figs. 7—9, probable distribution 8—10 + fragments; fig. 10, probable distribution 9—9 + fragments. —  $\times 3100$ .

As is evident from the table the most frequent configurations was  $3_{III} + 4_{II} + 1_I$ , which was found in 9 cells out of 23. Four other cells had  $2_{III} + 5_{II} + 2_I$ , the other six configurations were less frequent.

As may be seen from figs. 1—4 the trivalents were almost regularly V-shaped, the bivalents rod-shaped. The bivalents were often composed of chromosomes of unequal size or shape (figs. 1 and 3), and when more than one univalent was present these univalents often differed in size (figs. 1 and 4).

First anaphase in *bonariensis*  $\times$  *Langsdorfii* was characterized by the frequent occurrence of chromatin bridges between the separating chromosomes (figs. 7—10). The members of some bivalents and trivalents (fig. 7) separate with difficulty, the connections between the chromosomes become attenuated and finally disrupt. This disruption often leads to formation of fragments of different size but as in the *Crepis* hybrid *divaricata*  $\times$  *dioscorides* (MÜNTZING 1934) fragments are probably also formed without disruption. In several cases fragments were observed to lie close by a chromatin bridge which had not yet broken apart (fig. 10). Such fragments are probably formed by crossing over between homologous segments with a different position in the pairing chromosomes (cf. MC CLINTOCK 1933, MÜNTZING 1934).

Of ten different first anaphases, in which the total number of chromosomes could be counted, only four showed »clean» separation, the distributions being 8—10 (2 cells, fig. 5) and 7—11 (2 cells, fig. 6). In the other six cases there were complications, *i. e.* fragments or lagging chromosomes. In fig. 7 the distribution, when the remaining chromosome connections have disrupted, will probably be 8—10 together with quite a number of fragments between the poles. The same distribution, 8—fragments—10, will occur in figs. 8—9. In fig. 10 there will probably be 9 chromosomes at each pole and additional fragments. One chromosome in the upper anaphase group has already split. In fig. 11, finally, which represents a somewhat later stage, there are 8 chromosomes at one of the poles, 9 at the other. One chromosome and two fragments of different size are lagging between the anaphase groups. — At interphase eliminated chromosomes outside the nuclei were often observed. In fig. 12 the interphase nuclei contain 9 and 7 chromosomes respectively, some of which are already split. Between the nuclei there are three eliminated bodies which may represent one undivided and one divided chromosome. Division of univalents at I—A, however, must be very rare, as practically no



Figs. 11—22. Meiosis in *N. bonariensis*  $\times$  *Langsdorffii* (continued). — Fig. 11, first anaphase, distribution 8—1—9 + fragments. — Fig. 12, interphase. — Figs. 13—21, second metaphase; fig. 13, distribution 8—1—9; fig. 14, 8—10; fig. 15, 9—9; fig. 16, 7—11, figs. 17—21, fragments (and possibly divided univalents) in addition to the ordinary II—M chromosomes; fig. 22, second anaphase with an exceptional chromatin bridge. —  $\times 3100$ .

lagging chromosomes were observed at II—A. Of 71 second anaphases examined only 3 contained one lagging chromosome.

At second metaphase some cells (figs. 13—16) seemed to contain only normal chromosomes, in other cells there were fragments of different size and appearance (figs. 17—21). The fragments were, as a rule, outside the metaphase plates. In 29 cells, which were free from fragments, the chromosome numbers of both metaphase plates could be counted. The most frequent distribution (10 cells) was 8—1—9, *i. e.* one chromosome eliminated and 8 and 9 chromosomes resp. in the metaphase plates (fig. 13). In seven cells the distribution 8—10 (fig. 14) was observed and in seven other cases the distribution 9—9 (fig. 15). The distributions 7—11 (fig. 16) and 7—1—10 were less frequent (3 and 2 cells resp.). — The number of chromosomes in 100 II—M plates was counted and this gave the following values:

Number of chromosomes: . . . . .	7	8	9	10	11
Frequency: . . . . .	9	26	44	16	5

Nine is the most common number but the average value  $8.8 \pm 0.1$  is a little lower. This decrease is probably due to the amount of elimination observed.

In the cells containing fragments the number and nature of the chromosomes was more difficult to analyse. In fig. 17 one of the plates contains 9 normal chromosomes, the other one eight chromosomes of variable size in addition to one quite small chromosome, which probably represents a fragment. Another fragment has been eliminated and lies in the plasma some distance from the metaphase group first mentioned. In fig. 18 the metaphase groups contain 11 and 7 chromosomes respectively. One of the 11 chromosomes is conspicuously small and may be related to the fragment lying close to this plate. — In each of the metaphase plates represented in fig. 19 there is again a quite small chromosome in addition to the ordinary chromosomes. As no lagging chromosomes were observed at II—A these small chromosomes are probably fragments and not the halves of a univalent, which has divided at I—A. The same argument probably holds true for fig. 21. In this cell the fragments are lying at some distance from the plates, which contain 8 and 10 chromosomes respectively.

As already emphasized the second anaphases are as a rule quite regular. In a few cases, however, difficulties of separation and chromatin bridges were observed (fig. 22). These bridges were of a

similar type to those seen at I—A but were much less frequent and only occurred as exceptions.

The elimination of chromosomes and the formation of fragments are responsible for a frequent occurrence of micronuclei and microcytes in the tetrads of the *bonariensis*  $\times$  *Langsdorfii* hybrids. Of one hundred tetrads examined 55 per cent contained four cells, 41 per cent five cells and 4 per cent six cells. — Fifty tetrads of pure *N. bonariensis* all consisted of four cells.

The hybrid is probably not completely pollen sterile. One pollen sample examined contained 18 per cent apparently good grains. Female fertility has not yet been studied.

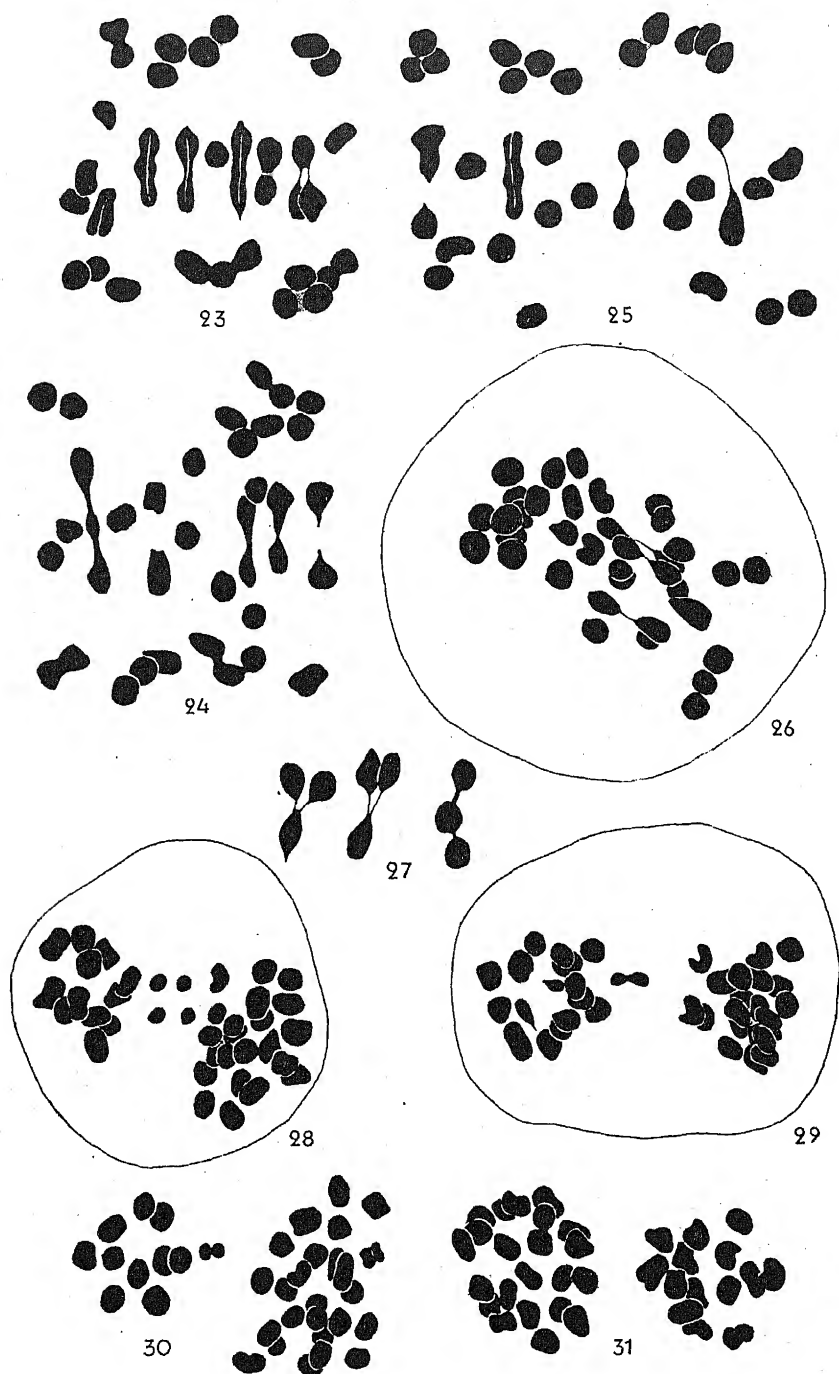
### NICOTIANA GLUTINOSA $\times$ TABACUM.

Though the hybrid *glutinosa*  $\times$  *tabacum* is the origin of the synthetic species »*N. digluta*» (CLAUSEN and GOODSPEED 1925) the cytology of the primary hybrid has not been studied in detail. This may be due to the fact that *digluta* arose by somatic doubling already in  $F_1$  and consequently not as the result of meiotic irregularities. Nevertheless, it seemed worth while studying the homology between the genomes of the two species and to compare the meiotic behaviour of the primary hybrid with that of the allopolyploid derivative, *digluta*.

In their paper of 1925 CLAUSEN and GOODSPEED briefly mention that chromosome behaviour in *glutinosa*  $\times$  *tabacum* closely parallels that found in the  $F_1$  *tabacum*  $\times$  *sylvestris* hybrids. In a later paper, however, CLAUSEN (1927) reports that the 36 chromosomes of *glutinosa*  $\times$  *tabacum* conjugate loosely according to the *Boreale* scheme.

This statement was confirmed by the present study. At first metaphase most of the 36 chromosomes (24 from *tabacum*, 12 from *glutinosa*) appear as univalents but as a rule a few bivalents are also present and even occasional trivalents may be observed (figs. 23—27). Most of the univalents were lying near the poles, the bivalents occupying the equatorial zone. The bivalents were loosely conjugated, and sometimes it was difficult to distinguish between a bivalent, the members of which had just separated, and two univalents. Therefore when studying the frequency of bivalents, it was necessary to determine both the number of quite unquestionable bivalents and the maximal number of bivalents in each cell. — Fifty different first metaphases were examined. The number of unquestionable bivalents ranged from





0 to 6 and was on the average 3.8. The frequency in the different classes was the following:

Number of bivalents: ....	0	1	2	3	4	5	6
Frequency: .....	2	1	3	14	15	10	5

The maximal number of bivalents in the same fifty cells ranged from 1 to 8 and was on the average 4.8. Thus  $4_{II} + 28_I$  may be considered to be the most typical I—M configuration in the *glutinosa*  $\times$  *tabacum* hybrid studied. Trivalents (figs. 23 and 27) were much rarer. In the fifty cells examined there were a total of 3 sure + 2 possible trivalents.

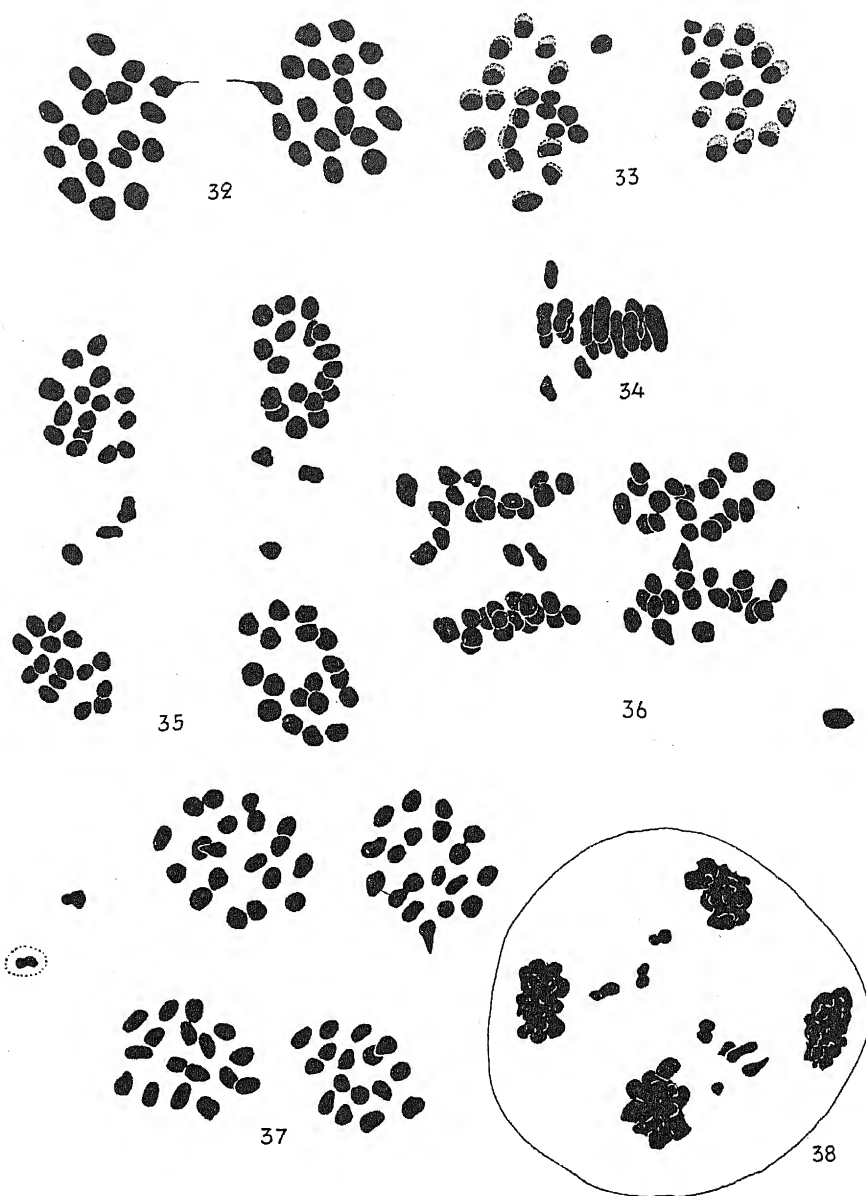
The univalents had a tendency to stick together in pairs or chains, a tendency which was also observed by ELVERS (1934) in the hybrid *Nicotiana glutinosa*  $\times$  *tomentosa*. It is very questionable if this phenomenon should be referred to as secondary association.

At first anaphase (figs. 28—31) the bivalent chromosomes separate and the univalents are distributed to the poles at random. Sometimes, but not often, univalents may divide at this stage. Fig. 28 shows two dividing chromosomes between the two anaphase groups, which contain 12 and 22 chromosomes respectively. In fig. 29 the chromosome distribution is  $14 + \frac{1}{2} - 1 - 20$ , i. e. in one of the anaphase groups there are two small chromosomes, which probably represent the halves of a divided univalent. Between the poles there is one lagging and elongated univalent. — Other distributions without divided univalents are represented in fig. 30 (25—11) and fig. 31 (22—14). — Though the first anaphases were relatively regular, the amount of lagging and division causes a frequent occurrence of micronuclei at interphase. Out of a hundred cells examined at this stage 57 contained one or several micronuclei, 43 cells only the two normal interphase nuclei.

At second metaphase the number of chromosomes of both plates could in some cases be counted. Fig. 32 shows a cell, in which both plates contain 18 chromosomes, in fig. 33, however, the sum of the chromosomes in the two plates is  $22 + 17 = 39$ , which shows that in this case some univalents have divided at I—A. — The presence of halves of univalents at II—M is also evident from fig. 34. — In another

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Figs. 23—31. Meiosis in *N. glutinosa*  $\times$  *tabacum*,  $F_1$ . — Figs. 23—26, first metaphase in side view (figs. 23—25 separately drawn); fig. 23,  $1_{III} + 3_{II} + 27_I$ ; figs. 24—25,  $4_{II} + 28_I$ ; fig. 26,  $3_{II} + 30_I$ ; fig. 27, one possible and two sure trivalents; figs. 28—31, first anaphase; fig. 28, distribution  $12 - \frac{1}{2} - 22$ ; fig. 29,  $14 + \frac{1}{2} - 1 - 20$ ; fig. 30,  $11 - 25$ ; fig. 31,  $14 - 22$ . —  $\times 3100$ .



Figs. 32—38. Meiosis in *N. glutinosa*  $\times$  *tabacum*,  $F_1$  (continued). — Figs. 32—34, second metaphase; fig. 32, polar view, 18 chromosomes in each plate; fig. 33, polar view, the two plates contain 22 and 17 chromosomes resp.; fig. 34, one II—M plate in side view. — Figs. 35—37, second anaphase, figs. 35 and 37 polar view (separately drawn), fig. 36 side view; the following distributions may be seen: fig. 35,  $\frac{15-3-15}{16-2-16}$ ; fig. 36,  $\frac{16-2-16}{18-18} + 1$  chromosome eliminated at I—A; fig. 37,  $\frac{16-17}{19-19} + 2$  eliminated chromosomes (or fragments); fig. 38, second telophase with lagging chromosomes. —  $\times 3100$ .

five cells at the same stage the total number of chromosomes was again higher than 36. The following distributions were found: 18—20, 19—19, 18—20 + 2 (eliminated chromosomes), 17—20 + 2 and 17—19 + 2. — The number of chromosomes in 52 single second metaphase plates was counted with the following result:

Number of chromosomes: . . . .	15	16	17	18	19	20	21	22	23
Frequency: . . . . .	1	7	9	13	12	6	3	—	1

The average number is 18.<sub>24</sub>. In spite of elimination at I—A, this value is higher than 18, which is no doubt due to division of univalents at I—A.

With regard to division of univalents different *Nicotiana* hybrids behave differently. In most cases the univalents do not divide at I—A but are distributed at random to the poles. In such cases, *e. g.* in *rustica* × *paniculata* (GOODSPEED, CLAUSEN and CHIPMAN 1926) and *sylvestris* × *tabacum* (GOODSPEED and CLAUSEN 1927) the total number of chromosomes in the two second metaphase plates does not exceed the somatic chromosome number. — In other *Nicotiana* hybrids occasional division of univalents at I—A has been reported. Such is the case, for instance, in aberrant forms of *N. alata* var. *grandiflora* (AVERY 1929), in the hybrids *N. digluta* × *glutinosa* and *digluta* × *tabacum* (CLAUSEN 1928) and in *N. »triplex»* × *sylvestris* (KOSTOFF 1933). — In *N. tomentosa* × *tabacum*, *F*<sub>1</sub>, however, division of univalents was rather frequent, and the II—M counts usually exhibited a total of more than 36 chromosomes (GOODSPEED and CLAUSEN 1928). With regard to division of univalents the present hybrid, *glutinosa* × *tabacum*, evidently behaves in the same way as *tomentosa* × *tabacum*.

At second anaphase lagging chromosomes often occurred which is to be expected since some univalents divide at I—A. In several II—A groups the total number and the distribution of the chromosomes could be observed. In the cell represented by fig. 35 the distribution was  $\frac{15-3-15}{18-3-18}$ . Evidently three chromosomes have divided at I—A and are now lagging. In fig. 36, which shows an early second anaphase in side view, the distribution is  $\frac{16-2-16}{18-18} + 1$  chromosome which has been eliminated at the first division. In fig. 37, again, the total number of chromosomes is 73 and not 72, as in the cases just mentioned. The four II—A plates contain  $\frac{17-16}{19-19}$  chromosomes and in addition there

are two eliminated chromosomes, one of which is rather small. The supernumerary chromosome must have arisen either by double division of a univalent or by fragmentation. That such processes may occur is also indicated by fig. 38, in which one of the lagging chromosomes is quite small. — Moreover, in sesquidiploid *tabacum*  $\times$  *sylvestris* plants WEBBER (1930) in the same way found evidence of double division or fragmentation of chromosomes.

The lagging and elimination of chromosomes is responsible for a frequent occurrence of micronuclei in the tetrads. Microcytes were also common and at the tetrad stage the pollen mother cells contained more often five cells than four. Of 50 »tetrads« examined 16 consisted of four cells, 23 of five and 11 of six cells. Not a single dyad was observed and consequently no unreduced male gametes are formed in this hybrid. The non-formation of unreduced gametes in the primary hybrid accords well with the fact that *digluta* arose by somatic doubling already in  $F_1$  and not by the union of unreduced gametes.

### NICOTIANA DIGLUTA.

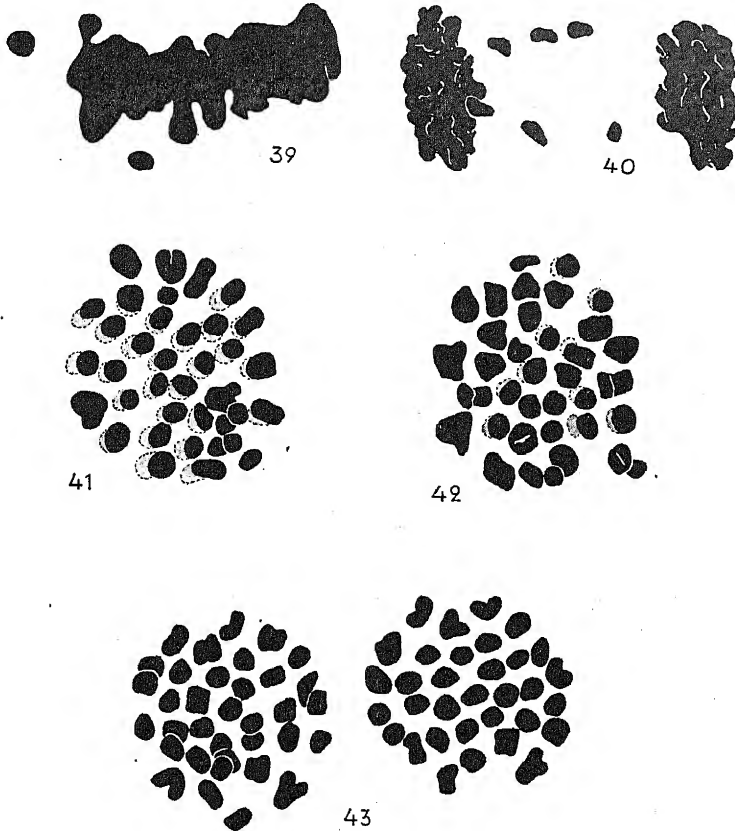
In order to compare the cytology of the primary hybrid *glutinosa*  $\times$  *tabacum* with that of the synthetic product, *digluta*, some slides of *digluta* were prepared. However, the *digluta* material available at this time of the year was not in a favourable condition for chromosome studies and only a few smears of p. m. c. from a single plant were obtained.

In the paper of 1925 CLAUSEN and GOODSPEED report that numerous counts of I—M figures in *digluta* all showed 36 bivalents, and that there seemed to be no univalents present. However, some irregularities in distribution were observed and this is again mentioned by CLAUSEN (1928) and by CLAUSEN and LAMMERTS (1929).

In the *digluta* plant examined by the present writer a small number of univalents were found to be present already at first metaphase (figs. 39 and 41—42) and at first anaphase lagging chromosomes were observed (fig. 40). At interphase micronuclei were frequent. — Besides the univalents only bivalents but no multivalents could be detected at I—M. An attempt was made to analyse a first metaphase in side view, but on account of the high chromosome number not all chromosomes could be distinguished. However, as many as 27 clear bivalents and 3 univalents could be discerned and no trivalents or quadrivalents were detected. — In several polar views (cf. figs. 41—42) the total number

of chromosomes could be counted and again the metaphase plates only consisted of bivalents and univalents.

Much to our surprise, however, the chromosome number of the plant examined was lower than the expected number 72. Not less

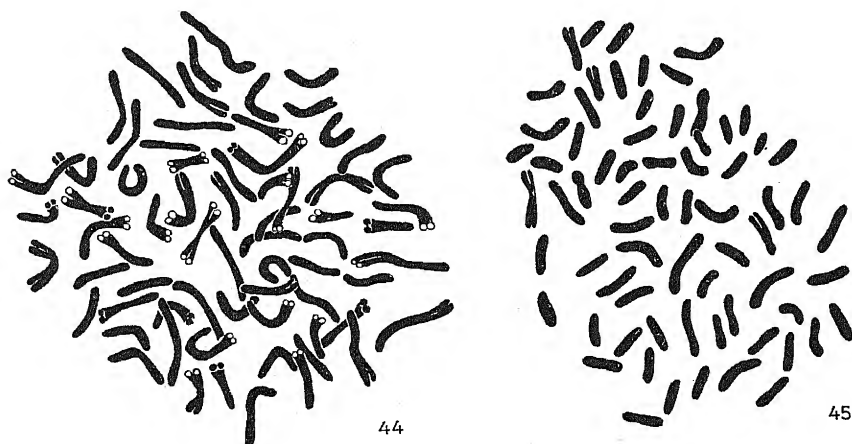


Figs. 39—43. Meiosis in *N. digluta*. — Fig. 39, first metaphase in side view; fig. 40, first ana—telophase with lagging chromosomes; figs. 41—42, first metaphase in polar view; fig. 41,  $33_{II} + 2_I$ ; fig. 42,  $32_{II} + 4_I$ ; fig. 43, first anaphase (separately drawn), the two plates contain 33 and 35 chromosomes. —  $\times 3100$ .

than four chromosomes were lacking, the chromosome number being 68. In fig. 41 there are most probably 33 bivalents and 2 univalents, in fig. 42 the chromosome complement consists of  $32_{II} + 4_I$ . The differences in size between the bivalents in figs. 41—42 are to be expected, since one of the constituting species, *N. tabacum*, is known to have chromosomes of rather different size (cf. CLAUSEN 1932). Therefore the big chromosomes in figs. 41—42 are bivalents and not multi-

valents. The correctness of the chromosome number 68 is definitely demonstrated by the early first anaphase represented in fig. 43. The two anaphase plates contain 33 and 35 chromosomes respectively.

The *digluta* plant examined was too old to allow fixation of root tips for counts of the somatic chromosome number. — In order to determine the chromosome numbers of some additional *digluta* plants, portions of *digluta* seeds were germinated, and the small root tips of the germinating seeds or the quite young seedlings were fixed. In addition, four plants were raised at Svalöf from *digluta* seeds kindly sent to me by Prof. CLAUSEN, and root tips of those plants were also



Figs. 44—45. Somatic chromosomes of two aberrant *digluta* plants. — Fig. 44,  $2n = 68$ ; fig. 45,  $2n = 69$ . —  $\times 3300$ .

fixed in chromacetic formalin. — The roots of the germinating seeds contained very few dividing cells and only three somatic plates, representing three different individuals (No. 28636, P. 10  $\times$  P. 4), could be counted. These plates were rather good, the chromosomes being rather contracted (fig. 45). The following  $2n$  values were found: 69, 68—69 and 67—69. With a very high degree of probability the somatic chromosome numbers of those root tips were 68 or 69 (fig. 45) and decidedly not 72.

The four plants raised at Svalöf (No. 28636, P. 10  $\times$  P. 9) were fixed at a later stage and therefore several root tips and somatic plates could be studied from each individual. In these roots the chromosomes were less contracted (fig. 44) than in the root tips of the germinating seeds. The following chromosome numbers were found:

Plant No. 1:	$\pm 68$	(bad fixation)
» 2:	68, 68, 68, $\pm 68$	
» 3:	68, 68, 68, 68—69, $\pm 68$	
» 4:	$\pm 68$	(bad fixation)

These counts were made by my technical assistant, Miss M. PALM, and were afterwards controlled by me. Though in most plates there were some obscure points, no plate had less than 67 or more than 69 chromosomes. Probably all four plants had  $2n=68$  (fig. 44). Consequently, also the P. 10  $\times$  P. 9 plants were aberrants with less than 72 chromosomes. Altogether a total of eight different *digluta* plants have been examined, including the one in which meiosis was studied. All these plants, which belong to the  $F_6$  generation, had either 68 or 69 chromosomes instead of 72.

### DISCUSSION.

As is well known many experimentally produced amphidiploids are not cytologically stable. If the chromosomes of the primary hybrid are partially homologous, interspecific pairing may occur in the amphidiploid, and multivalents may be formed. Irregular disjunction of multivalents leads to gametes with deviating chromosome numbers and a certain proportion of aberrants in the progeny. Such is the case, e. g. in the amphidiploid *Nicotiana rustica*  $\times$  *paniculata* studied by LAMMERTS (1931, 1932). As in *N. digluta* the normal chromosome number is 72 (48 *rustica* + 24 *paniculata* chromosomes) but in the progenies a certain proportion of the plants have more or less than 72 chromosomes. — Other cases of cytologically unstable amphidiploids, in the progenies of which aberrants appear, are represented by *Digitalis mertonensis* (BUXTON and NEWTON 1928), *Primula Kewensis* (NEWTON and PELLEW 1929) and the amphidiploid *Crepis rubra*  $\times$  *foetida* (POOLE 1932). In several other cases meiosis is irregular enough to cause the formation of aberrants in the progeny, though the production of such individuals with deviating chromosome numbers has not actually been demonstrated.

Gametes with deviating chromosome numbers may be formed not only by irregular disjunction of multivalents but also as a result of non-conjunction. This seems to be the case with *N. digluta*. The occurrence of *digluta* plants which lack as many as four chromosomes has been demonstrated in the present paper. These aberrants may have arisen either by elimination of chromosomes in somatic divisions or by formation of aberrant gametes. The latter alternative is the



most probable one, since distributional irregularities at meiosis in *digluta* have been reported several times (CLAUSEN and GOODSPEED 1925, CLAUSEN 1928, CLAUSEN and LAMMERTS 1929). Such irregularities, indeed, were observed already in the amphidiploid  $F_2$  plants. — In the 68-chromosome *digluta* plant studied no multivalents but several univalents were observed at first metaphase. It is rather probable that univalents may be present at meiosis also in the regular 72-chromosome *digluta* plants, and that this non-conjunction is responsible for the production of aberrant *digluta* individuals. As no multivalents were observed in the aberrant plant studied, they are probably lacking also in normal *digluta*. This is not unexpected since chromosome pairing in the primary hybrid was found to be very weak. Further, the tendency to form multivalents does not seem to be very pronounced in *Nicotiana*. According to ELYERS (1934) the frequency of multivalents in the amphidiploid *glutinosa* + *tomentosa* is quite low and not corresponding to the number of bivalents in the primary hybrid.

The cause of non-conjunction between homologous chromosomes is more difficult to understand. However, extra chromosomal influences frequently influence chromosome pairing. In amphidiploids such influences may be plasmatic and due to incongruity between the plasma of the mother species and chromosomes of the other species. Like *N. digluta*, the amphidiploid wheat—rye hybrids show a certain amount of non-conjunction and resulting irregularities, though all chromosomes have homologous partners and should form only bivalents (LEVITSKY and BENETZKAIA 1929, 1931).

In any case the occurrence of *digluta* plants with aberrant chromosome numbers definitely demonstrates that also this amphidiploid is not cytologically stable. — The aberrant *digluta* plants are all  $F_6$  individuals obtained after crosses between different  $F_5$  plants. Prof. CLAUSEN has kindly informed me that the  $F_2$ ,  $F_3$ ,  $F_4$  and  $F_5$  generations were raised from self-pollinated seeds. — As the eight *digluta* plants examined had all  $\pm$  68 chromosomes instead of 72, this seems to indicate that a new derivative line of *digluta* has arisen, in which some chromosomes have been lost. This possibility of course needs more extensive investigations. It should be pointed out, however, that the result of crosses between *digluta* and *tabacum* described by CLAUSEN and LAMMERTS in 1929 indicate that the *digluta* plants used for the crosses already at that time had less than 72 chromosomes. Besides a haploid *tabacum* plant, arisen through haploid merogony, three other *digluta*  $\times$  *tabacum* plants were examined cytologically. The *digluta*  $\times$

*tabacum* hybrids should have  $2n = 60$  (36 *digluta* + 24 *tabacum* chromosomes) but of the three plants examined two had  $2n = 57$ , the third plant 58 chromosomes. In view of the present results this strongly indicates that the *digluta* plant used for the crosses had only about 68 chromosomes instead of 72 ( $34 + 24 = 58$ ). — One year earlier, however, CLAUSEN (1928) described hybrids between *digluta* and its constituting species, *glutinosa* and *tabacum*, which had the expected chromosome numbers (48 and 60 respectively).

The loss of several chromosomes in *digluta* may occur without conspicuous morphological alterations since *digluta* is polyploid and losses of chromosomes have less effect in polyploids than in diploids. *N. digluta* probably reacts in a similar way to chromosome alterations as the amphidiploid *rustica*  $\times$  *paniculata*. According to LAMMERTS (1932) the derivative lines of this amphidiploid were uniform in spite of the chromosomal irregularities and the plants with more or less than 72 chromosomes were indistinguishable from the others.

Occasional trivalents at meiosis have been observed in several species hybrids in *Nicotiana*, e. g. in the sesquidiploid *tabacum*  $\times$  *sylvestris* (WEBBER 1930), in *glutinosa*  $\times$  *tomentosa* (ELVERS 1934), and probably in *Nicotiana* «*triplex*» studied by KOSTOFF (1932). A low frequency of trivalents was also found in the *glutinosa*  $\times$  *tabacum* hybrid described in the present paper. With regard to chromosome behaviour the hybrid *bonariensis*  $\times$  *Langsdorfii* differs strikingly from all these cases and from all other *Nicotiana* hybrids hitherto studied by the high frequency of trivalents at first metaphase. On the average not less than 44 per cent of the chromosomes were associated to trivalents at this stage.

Practically no material of the parent species was available at the time the hybrid was studied. Only tetrads of *N. bonariensis* were examined and found to be quite regular without microcytes and micronuclei. Therefore, meiosis in *bonariensis* is most probably regular and only bivalents formed. Also in the other parent species *Langsdorfii*, which has often been used for crosses, only normal bivalents are present at first metaphase (cf. KOSTOFF 1930, Plate I, fig. 2).

The frequent trivalent associations in the hybrid must be due to structural hybridity, some chromosomes of the one parent being homologous to parts of two chromosomes of the other parent species. This is the explanation given for several other species hybrids, in which multiple associations have been observed, viz. in hybrids of *Polemonium* and *Viola* (J. CLAUSEN 1931 a, 1931 b), *Godetia* (HÅKANSSON 1931),

*Datura* (BERGNER and BLAKESLEE 1932, BLAKESLEE 1932), *Triticum* and *Aegilops* (KIHARA and LILIENFELD 1932). The chromosome rings in *Oenothera* probably belong to the same category and also the cases of multiple chromosome association in intraspecific hybrids (cf. HÅKANSSON 1931). — This ever-increasing material emphasizes the fact that the evolution of species and biotypes has frequently been accompanied by structural changes in the chromosomes.

The somatic chromosomes of *Nicotiana Langsdorfii* and *bonariensis* were not studied by the present writer, but Dr. PRISCILLA AVERY has kindly informed me that the idiograms of the two species are somewhat different, and that within each species there are chromosomes of different size and morphology. These differences could not be studied in detail at meiosis, but the multiple associations in the  $F_1$  hybrid strongly indicate that translocations or segmental interchanges are at least in part responsible for the differences between the idiograms of *Langsdorfii* and *bonariensis*.

Pairing between chromosomes or parts of chromosomes is generally regarded as evidence of homology, but especially during the prophase of meiosis also non-homologous pairing may occur (MC CLINTOCK 1933). The multivalent associations of some species hybrids might possibly be attributed to such non-homologous pairing. This, however, is unlikely already for the reason that non-homologous associations seldom persist till diakinesis and first metaphase (MC CLINTOCK l. c.). Further, if associations were at random between any chromosomes, no special chromosome configurations should be more frequent than others. — In the *bonariensis*  $\times$  *Langsdorfii* hybrid, however, the configuration  $3_{III} + 4_{II} + 1_I$  was found to be significantly more frequent than the average of the other configurations. This can only be explained as due to pairing between homologous chromosomes and homologous parts of chromosomes. — If the two ends of each *bonariensis* and *Langsdorfii* chromosome are represented by letters, the two species in the simplest case may have the following constitution and pairing relations:

<i>bonariensis</i> :	AB	CD	EF	GH	IJ	KL	MN	OP	QR
<i>Langsdorfii</i> :	AD	ES	TF	GJ	KL	MN	OP	QR	UV

$\begin{array}{cccccccccc} & \diagdown & & \diagup & & \diagdown & & \diagup & & \diagup \\ & & & & & & & & & \end{array}$

Such a constitution would lead to formation of  $3_{III} + 4_{II} + 1_I$ . No doubt, however, the homologous segments are distributed in a more complicated way.

The presence of homologous segments with different position in

relation to the spindle fiber insertion is probably responsible for the formation of chromatin bridges and fragments at first anaphase. These are probably of the same type as those studied in the *Crepis* hybrid *dioscoridis*  $\times$  *divaricata* (MÜNTZING 1934). If that is correct, the chromatin bridges represent double attachment chromosomes formed by crossing over between homologous segments. As discussed in detail in the *Crepis* paper, fragments without attachment constriction will be formed at the same time, and other fragments may arise by breakage of the chromatin bridges.

The important point is that such processes may lead to a multitude of new chromosome types, some of which may survive. The observations in *Nicotiana bonariensis*  $\times$  *Langsdorfii*,  $F_1$ , further support the theory that changes in chromosome structure often arise at meiosis in species hybrids.

### SUMMARY.

1) First metaphase in *Nicotiana bonariensis*  $\times$  *Langsdorfii*,  $F_1$ , is characterized by a regular occurrence of trivalents in addition to bivalents and univalents. The most frequent chromosome configuration observed was  $3_{III} + 4_{II} + 1_I$ . The formation of trivalents must be due to structural differences between the genomes of the parent species.

2) At first anaphase chromatin bridges between the anaphase chromosomes were frequently observed. These bridges probably represent double attachment chromosomes formed by crossing over between homologous segments in structurally dissimilar chromosomes. Fragments are formed at the same time and other fragments by breakage of the double attachment chromosomes.

3) In *N. glutinosa*  $\times$  *tabacum*,  $F_1$ , the primary hybrid of the synthetic species *N. »digluta*, chromosome pairing is rather weak,  $4_{II} + 28_I$  being the most frequent configuration. Occasional trivalents were also observed. The distribution of the chromosomes in the meiotic divisions is relatively regular, and no unreduced gametes are formed in the pollen. This is in accordance with the fact that *digluta* arose by somatic doubling and not by the union of unreduced gametes.

4) Meiosis in one  $F_6$  plant of *N. digluta* was examined. At first metaphase no multivalents but only bivalents and univalents were present. The chromosome number of this plant was only 68 and not 72, the normal number of *digluta*. The somatic chromosome numbers in seven other  $F_6$  individuals were also found to be 68 or 69. This demonstrates that *N. digluta*, like several other amphidiploids, is not

cytologically stable and indicates that derivative lines with other chromosome numbers than 72 may arise.

Svalöf, Cyto-Genetic Department of the Swedish Seed Association, December 1934.

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# KOMPLEXE UND HOMOLOGE MUTATIONEN

## INSBESONDERE BEI *PHASEOLUS VULGARIS*, *PH. MULTIFLORUS* UND *PISUM SATIVUM*

VON HERBERT LAMPRECHT

SAATZUCHTANSTALT WEIBULLSHOLM, LANDSKRONA

(With a summary in English)

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VOR kurzem ist von mir in dieser Zeitschrift über eine Mutation mit einfachen Blättern bei *Phaseolus vulgaris* berichtet worden (LAMPRECHT 1935 b). Hierbei hat auch schon die Vererbungsweise dieser Mutation klargelegt werden können. Seither sind von mir abermals zwei Mutationen von *Ph. vulgaris* angetroffen worden, deren Beschaffenheit und Auftreten das Wesen der *unifoliata*-Mutationen bei den Arten *Ph. vulgaris*, *multiflorus* (eventuell auch *angularis*) und *Pisum sativum* in etwas neuem Lichte erscheinen lässt. Die angestellten Beobachtungen machen es höchst wahrscheinlich, dass gewisse homologe Gene in diesen Arten eine besonders ausgeprägte Tendenz zu komplexen Mutationen aufweisen.

Über die früher bei *Ph. vulgaris* studierte *unifoliata*-Mutation (LAMPRECHT 1935 b) wäre — kurz zusammengefasst — etwa folgendes anzuführen. Die Mutante weicht von der Sorte, in der sie angetroffen worden ist, vor allem durch die Gestaltung der Blätter ab. Diese sind an ein und derselben Pflanze stets teils einfach, ungeteilt, teils zwei- oder dreiteilig. Die dreiteiligen Blätter dieses *unifoliata*-Typus sind aber von den gewöhnlichen dreiteiligen Blättern von *Ph. vulgaris* immer sicher dadurch zu unterscheiden, dass 1. die Basis derselben gerade quer bis schwach herzförmig statt nach unten verschmälert ist, 2. der Blattstiel nur ein Paar Stipellen kurz unter der Basis des Blattes trägt und 3. eventuell auftretende (ein oder zwei) seitliche Blättchen stets unmittelbar oberhalb dieser Stipellen entspringen und nicht, wie beim gewöhnlichen Blatt, ihren Ursprung weiter unten bei einem zweiten Paar Stipellen am Blattstiel haben. In Fig. 1 sind einige Blätter der bei diesen *unifoliata*-Pflanzen auftretenden Typen abgebildet.

Die in Rede stehende *unifoliata*-Mutation hat sich als vollkommen fertil erwiesen und das Studium einer Kreuzung (Nr. 169) zwischen



diesem Typus und einer Bohnen-Linie mit normalen Blättern hat dargestellt, dass der *unifoliata*-Charakter gegenüber dem gewöhnlichen dreiteiligen Blatt einfach rezessiv ist. Das hierfür verantwortliche Genpaar wurde von mir mit *Uni—uni* bezeichnet. In bezug auf sonstige Details sei auf die Originalarbeit verwiesen.

Im Jahre 1934 sind nun bei der Inspektion einer Vermehrung der allbekannten Sorte Hundert für Eine abermals zwei Typen von Mutationen entdeckt worden. Über

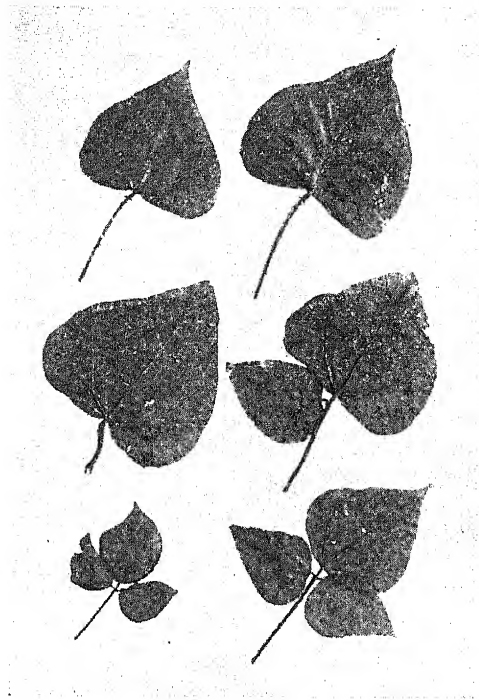


Fig. 1. Die verschiedenen bei *uni—uni*-Pflanzen von *Ph. vulgaris* auftretenden Blatttypen.

den einen dieser beiden Typen ist nicht viel zu sagen. Er zeigte ganz die gleichen Blattcharaktere wie der oben und früher (LAMPRECHT 1935 b) eingehender beschriebene *unifoliata*-Typus, nur dass hier die übrigen Charaktere der Mutante mit jenen der Sorte Hundert für Eine übereinstimmen, in der sie angetroffen worden ist. Bei dem früher beschriebenen Typus sind gegenüber der Muttersorte mehrere geringere Abweichungen vorhanden gewesen, weshalb der Ursprung derselben etwas zweifelhaft erschien. Beim vorliegenden Typus herrscht aber — abgesehen von den *unifoliata*-Blättern — anscheinend vollkommene Übereinstimmung mit der Muttersorte. So haben

die Samen die gleiche Form, die gleiche Testafarbe, Maisgelb, der Formel *PP cc JJ GG bb vv rr* entsprechend, die Hülsen haben gleiche Form und Beschaffenheit u. s. w. Bei dieser Form scheint die Mutation also nur das Genpaar *Uni—uni* betroffen zu haben. Von dieser Form wurden unter 375,000 Individuen der Muttersorte nur zwei angetroffen. Die in Frage stehenden Pflanzen zeigten anscheinend ganz normale Fertilität.

Von weitaus grösserem Interesse ist die zweite Mutation, die in der gleichen Sorte und unter denselben Individuen (375,000) in zusammen

neun Individuen angetroffen worden ist. Bei diesen vollkommen sterilen Individuen scheint die Mutation gleichzeitig wenigstens drei

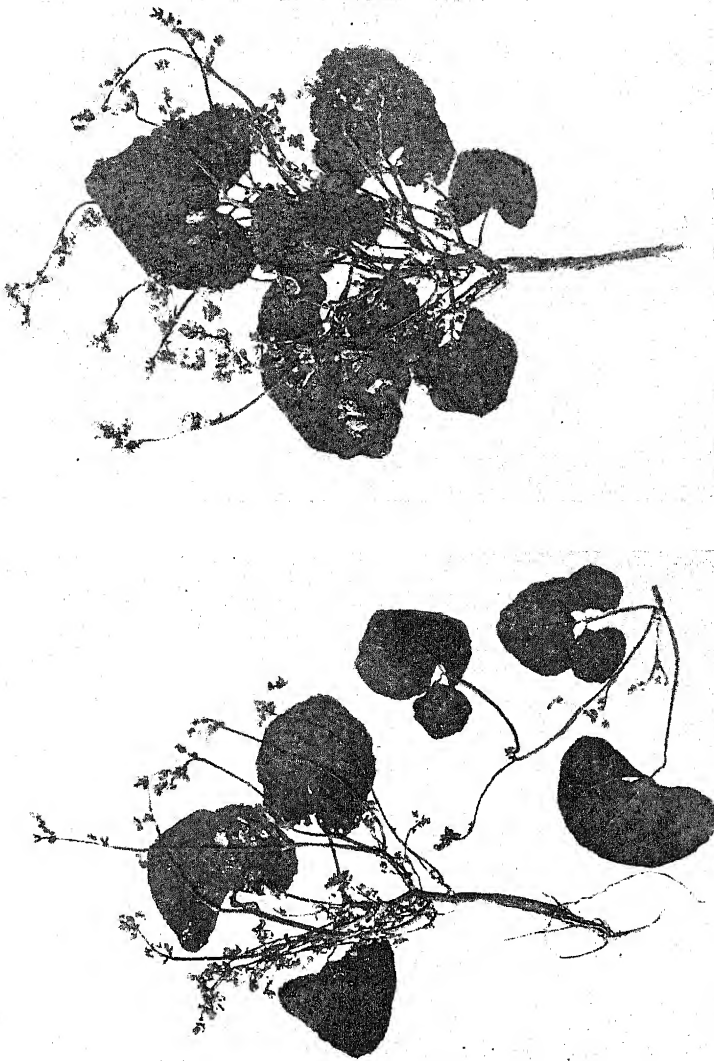


Fig. 2. Teile einer der sterilen Pflanzen von *Ph. vulgaris*, die 1934 in der Sorte Hundert für Eine als Komplexmutanten aufgetreten sind. Man beachte die Blätter vom *unifoliata*-Typus, die verzweigten Infloreszenzen und die sterilen Blüten.

Genpaare betroffen zu haben. In Fig. 2 ist eine solche Pflanze, der besseren Übersicht halber in drei Teile zerlegt, abgebildet.

Aus Fig. 2 geht unmittelbar hervor, dass wir es hier auch mit einem *unifoliata*-Typus zu tun haben. Die Blätter zeigen allerdings nicht dieselbe Form wie die des früher untersuchten *unifoliata*-Typus (Fig. 1)

sondern sind an ihrer Spitze stumpf abgerundet und etwas breiter als lang, aber sie zeigen denselben *unifoliata*-Plan. Es kommen also auf derselben Pflanze einfache, ungeteilte wie auch zwei- und dreiteilige Blätter vor; die Basis der Blätter ist gerade quer bis schwach herzförmig und auf den Blattstielen ist immer nur ein Paar Stipellen vorhanden. Derselbe Blatttypus charakterisiert auch die erste, vorhin erwähnte Mutante von Hundert für Eine. Es dürfte kaum ein Zweifel darüber bestehen können, dass dieser Charakter auf das schon früher festgestellte Genpaar *Uni—uni* zurückzuführen ist, und demnach einfache monohybride Vererbung aufweisen wird.

Eine zweite vom Normaltypus abweichende Eigenschaft, die unmittelbar aus dem Bilde zu entnehmen ist, ist der Bau der Infloreszenzen. Diese bestehen hier nicht aus einfachen Trauben sondern aus homotaktisch zusammengesetzten solchen. Von den Nodien der Trauben entspringen also wiederum seitliche Trauben. Diese Eigenschaft, Verzweigung der Infloreszenzen, ist von mir früher auf ihre Vererbung hin untersucht worden (LAMPRECHT 1935 a), wobei sich herausgestellt hat, dass das Eigenschaftspaar unverzweigte—verzweigte Infloreszenz auf ein Genpaar *Ram—ram* zurückzuführen ist. Die in Frage stehende Mutation hat demnach ausser *Uni—uni* noch ein zweites, bereits vorher analysiertes Genpaar, *Ram—ram*, getroffen.

Am Habitusbild der Mutante in Fig. 2 können noch einige weitere Abnormitäten beobachtet werden. Der Stamm zeigt in seinem unteren Teil (am linken Bilde der Figur ersichtlich) eine Fasciation. Diese ist nicht stark ausgebildet, aber doch deutlich genug um mit Sicherheit als solche angesprochen werden zu können. Ich besitze eine ganze Reihe von *fasciata*-Typen von *Phaseolus vulgaris*, aber das Studium ihrer Vererbung hat bisher Schwierigkeiten verursacht, da meistens alle Übergänge zu normalen Typen aufgetreten sind, eine Erscheinung, die auch von anderen Pflanzen, z. B. *Antirrhinum*, bekannt ist.

Eine andere vom Normaltypus abweichende Erscheinung ist ferner, dass die Infloreszenzen schon vom ersten Verzweigungspunkt des Stammes an volle Entwicklung erreichen, während dies gewöhnlich erst vom zweiten bis dritten Verzweigungspunkt an der Fall zu sein pflegt.

Schliesslich sieht man, dass sich aus keiner der zahlreichen Blüten eine Hülse zu entwickeln beginnt; die Pflanze scheint also offenbar steril zu sein. Die weitere Entwicklung dieser Mutanten und eine Untersuchung der Blütenelemente bestätigt dies. Die Vor- und Kelchblätter sowie die Fahne haben etwa das Aussehen normaler Blüten. Vielleicht ist letztere durchschnittlich etwas kürzer. Die Flügel sind

dagegen deutlich verkürzt und mit der Spiraltöhre nicht seitlich, sondern erst an der Basis verwachsen. Ab und zu findet man in Blüten den oberen Teil eines oder beider Flügel etwas in die Spiraltöhre eingezogen. Dies ist nur dadurch möglich, dass das Spiraltrohr an seinem oberen Ende unvollständig ausgebildet ist; es ist mehr oder weniger stark offen. Infolge dessen hat man in Knospen gleich nach dem Öffnen der Fahne schon freien Einblick zu den Staubgefässen.

Das Androeceum zeigt nur eine unbedeutende Abweichung von der normalen Beschaffenheit. Die Staubfäden zeigen nicht die übliche Spiralkrümmung, was aber wohl mit der abnormen Ausbildung des Spiraltrohres zusammenhängen dürfte; sie sind mehr oder weniger gerade. Die Staubbeutel erscheinen gut von Pollen erfüllt und dieser zeigt auch unter dem Mikroskop normales Aussehen.

Das Gynoeceum ist dagegen hochgradig missbildet. Es besteht merkwürdigerweise aus drei Fruchtblättern. Fig. 3 zeigt ein solches Gynoeceum. Wie aus dieser ersichtlich ist, zeigen die drei Fruchtblätter, die am Grunde miteinander etwas verwachsen sind, nicht die sonst übliche Gestalt und Spiralkrümmung. Sie sind mehr oder weniger gerade, stets offen, enthalten eine variierende Anzahl Samenanlagen und ihre Narbe ist mehr oder weniger reduziert oder fehlt mitunter ganz. Die Aussenseite der Fruchtblätter ist wie gewöhnlich behaart, bei der Mutante vielleicht etwas reichlicher.

Diese Fruchtblätter sind, auch wenn ab und zu eine Verwachsung stattfinden könnte, vollkommen steril. Mitunter kommt es vor, dass die Fruchtblätter einzelner Blüten etwas weiterwachsen, sodass sie bei reifenden Pflanzen eine Länge von bis zu ungefähr 2 cm erreichen können. Niemals hat jedoch in diesen eine Spur zur Entwicklung von Samen beobachtet werden können. In Fig. 4 sind einige Infloreszenzweige im Reifestadium abgebildet, von denen drei solche weiter gewachsene Fruchtblätter tragen. Erwähnt sei dass ich die gleiche Erscheinung auch bei einigen sterilen Individuen in Kreuzungen zwischen *Ph. vulgaris* und *multiflorus* beobachtet habe.

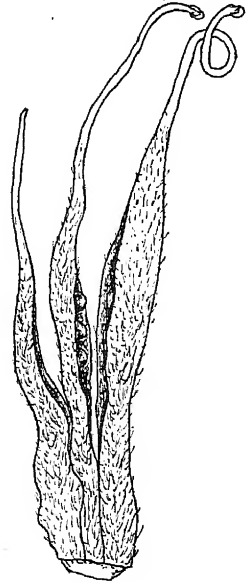


Fig. 3. Das Gynoeceum der Komplexmutante von *Ph. vulgaris*; drei zum grossen Teil offene, missbildete, vollkommen sterile Fruchtblätter.

Eine Diskussion der vorstehend mitgeteilten Mutationserscheinungen bei *Ph. vulgaris* wird gemeinsam mit den entsprechenden Verhältnissen bei *Ph. multiflorus* und *Pisum sativum*, nach Referierung dieser, folgen.

Über eine Mutation bei *Ph. multiflorus*, die in gewissen Hinsichten mit den vorhin für *Ph. vulgaris* beschriebenen analoge Erscheinungen aufweist, hat D. RIESER (1924) berichtet. Hier sei das wichtigste über diese Mutation, die von RIESER in nur einem einzigen Exemplar hat studiert werden können, wiedergegeben.

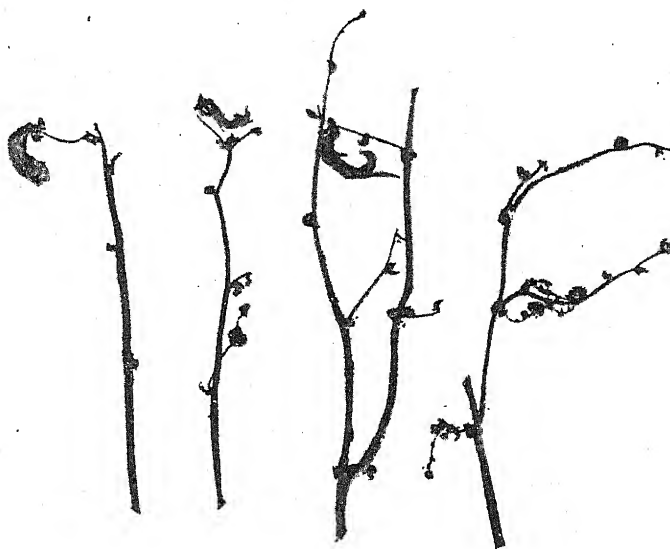


Fig. 4. Infloreszenzteile der Komplexmutante von *Ph. vulgaris* im Reifestadium; die Blüten sind vertrocknet, aber in einzelnen sind die drei Fruchtblätter etwas weiter gewachsen ohne dass jedoch eine Spur zur Entwicklung von Samen beobachtet werden kann.

Vorweg sei erwähnt, dass RIESER ausser einer morphologischen Beschreibung der in Frage stehenden Pflanze auch eine recht eingehende anatomische Untersuchung derselben — im Vergleich mit normalen Exemplaren — vorgenommen hat. Letztere Untersuchung hat insofern zu keinen Resultaten von Interesse geführt, als keine Abweichungen im anatomischen Bau haben konstatiert werden können.

In bezug auf die Gestaltung der Blätter wird konstatiert, dass die Mehrzahl derselben ungeteilt ist, die übrigen sind entweder zwei- oder dreiteilig. Die ungeteilten Blätter sind wesentlich grösser als die Blätt-

chen der gewöhnlichen dreiteiligen Blätter. RIESER erwähnt hierzu, dass die Vergrößerung des *unifoliata*-Blattes eine Kompensation mit Hinsicht auf die assimilierende Fläche darstelle. Bei den zwei- und dreiteiligen Blatttypen der Mutation sind das oder die beiden unteren Blättchen kleiner und gewöhnlich zum Teil vom grossen Terminalblättchen überdeckt. In seiner Fig. I, die hier als Fig. 5 wiedergegeben ist, bildet RIESER drei Blätter ab. Das linke bezeichnet er als »Normales Blatt von *Phaseolus multiflorus*«, das mittlere, zweiteilige als »Intermediäres (atavistisches) Blatt von *Ph. multiflorus*« und das rechte als »Blatt der neuen Mutation: *unifoliata*«.

Laut RIESERS Beschreibung sollten nun alle diese drei Typen auf der *unifoliata*-Pflanze vorkommen, wobei zu beachten ist, dass das

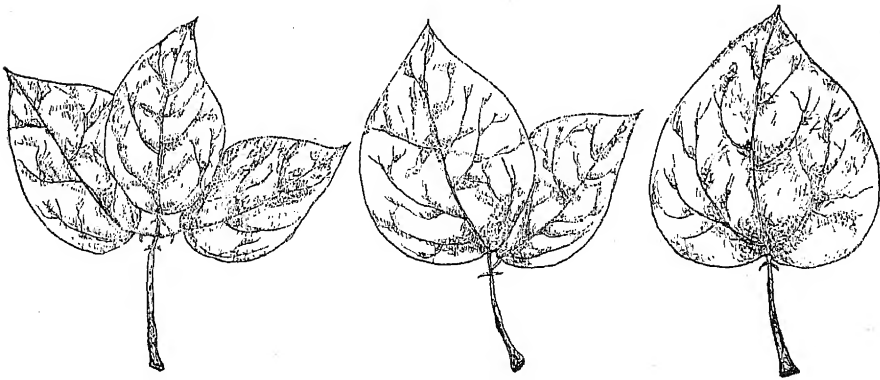


Fig. 5. (= RIESERS Fig. I). Links normales Blatt von *Ph. multiflorus* (»laut RIESER«), in der Mitte und rechts zwei Blatttypen der Mutation *unifoliata*.

linke Blatt mit dem normalen *multiflorus*-Blatttypus übereinstimmen soll. So schreibt RIESER (l. c. p. 8): »La série de formes entre la feuille normale et la feuille unifoliée est donc complète«, und ferner (l. c. p. 20): »Comme nous l'avons déjà dit, on trouve également sur la plante en mutation quelques feuilles à trois folioles absolument identiques aux feuilles des plantes normales«. In bezug auf die Stipellen sagt RIESER, dass an der Basis des Stielchens, kurz unter dem Blattrand links und rechts eine Stipelle vorhanden ist.

RIESERS Fig. I (hier = Fig. 5) und seine Äusserung in bezug auf die vollkommene Übereinstimmung der dreiteiligen Blätter der Mutation mit normalen *multiflorus*-Blättern sind in gewisser Hinsicht höchst wahrscheinlich fehlerhaft. Ein Blatt wie das links in seiner Fig. I abgebildete habe ich bisher noch bei keiner Rasse von *Ph. multiflorus* angetroffen. In Fig. 6 ist je ein Blatt von drei verschiedenen Sorten

dieser Art abgebildet, die die verbreitetsten in Mittel- und Nordeuropa sind. Wie aus dieser Fig. hervorgeht, ist erstens der Blattstiel zwischen der Basis des Terminalblättchens und der Ursprungsstelle der beiden seitlichen Blättchen erheblich, etwa viermal, länger als in RIESERS Fig. Ferner bildet RIESER vier Paar Stipellen ab, ein Paar kurz unter der Basis des Terminalblättchens, ein Paar kurz unter der Ursprungsstelle der beiden seitlichen Blättchen und schliesslich je ein Paar, entspringend von den Stielen der letzteren. Stipellen der letzteren Art habe ich bisher weder bei *Ph. multiflorus* noch bei *Ph. vulgaris* angetroffen. Da die von mir in Fig. 6 abgebildeten drei Blätter von *Ph. multiflorus*, wie erwähnt, den in Mittel- und Nordeuropa am

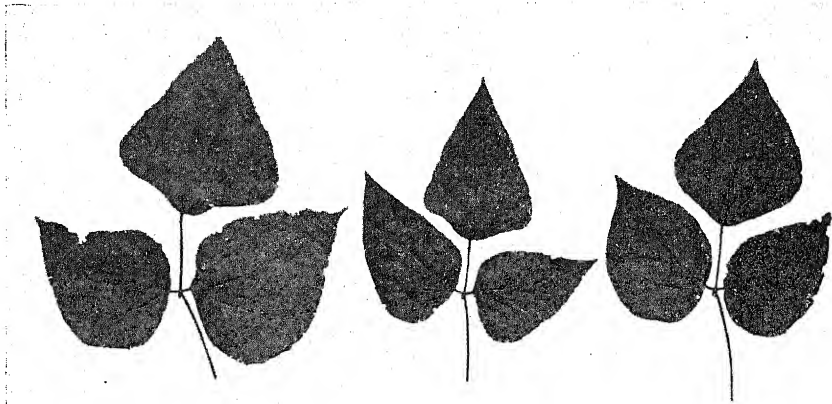


Fig. 6. Normale Blätter von drei verschiedenen Sorten von *Ph. multiflorus*.

meisten gebauten Sorten entsprechen, erscheint es zumindest höchst wahrscheinlich, dass hier ein Irrtum RIESERS vorliegt.

Die Blätter von RIESERS Mutante tragen nur ein Paar Stipellen, und zwar kurz unter der Basis des *unifoliata*-Blattes bzw. an der Ursprungsstelle eventuell auftretender seitlicher Blättchen. Hiervon habe ich mich an einem Herbariumbogen überzeugen können, der einen Teil des RIESERSchen Original Exemplares trägt und den ich durch die Vermittlung des Lunder Bot. Museums erhalten habe. Die Etikette des Bogens trägt folgenden Text: »Ex Herbario Universitatis Lousoun. *Phaseolus multiflorus* WILLD. mutatio *unifoliata* (cf. DOLF RIESER: Sur une mutations unifoliée de *Ph. multiflorus*. Diss. Lousounae 1924). Cult. in Horto Lousounnensi. Prof. A. MAILLEFER».

Die Blätter der RIESERSchen *unifoliata*-Mutante unterscheiden sich demnach in gleicher Weise von jenen der normalen *multiflorus*-Pflan-

zen wie die Blätter meiner *unifoliata*-Mutante von *Ph. vulgaris* sich von den normalen Blättypen dieser Art unterscheiden, d. h. bei beiden in Frage stehenden Mutanten gibt es sowohl ein-, zwei- und dreiteilige Blättypen, aber stets nur ein Paar Stipellen kurz unter dem Terminalblättchen und wenn ein oder zwei seitliche Blättchen auftreten, so entspringen diese in unmittelbarem Anschluss an dieses Stipellenpaar (vergleiche übrigens Fig. 1 und 2).

In noch einer Hinsicht zeigt die RIESERSche Mutante eine wesentliche Abweichung von dem Normaltypus von *Ph. multiflorus*. Es gilt dies für die Blüte. Die Infloreszenzen zeigen den normalen Bau, nicht verzweigte Trauben. An Stelle der Blüten findet man indessen Büschel von kleinen, 3 bis 5 mm langen grünen Blättchen. Fig. 7 ist eine Wiedergabe von RIESERS Fig. XV, die eine solche Infloreszenz zum Teil abbildet (Zeichnung nach der Natur; vergrössert). Sämtliche Elemente der Blüte sind in solche Blättchen, von etwas verschiedener Grösse, umgewandelt. Laut RIESER zeichnen sich diese Blättchen durch eine sehr hervortretende Nervatur aus. Irgend welche Reste von Gynoeceum- oder Androeceum-Charakteren haben an denselben nicht gefunden werden können. Wir haben es also hier mit einer Phyllodie sämtlicher Blütenelemente zu tun. Selbstverständlich sind diese umgewandelten Blüten vollkommen steril.

Eine genetische Untersuchung dieser Mutante hat von RIESER nicht ausgeführt werden können, teils wegen der Sterilität der Mutante, teils da keine Heterozygoten zur Verfügung gestanden sind. Es dürfte aber als sicher angenommen werden können, dass die RIESERSche Mutante teils einer Komplexmutation ihre Entstehung zu verdanken hat, an der wenigstens zwei Gennpaare beteiligt sind, eines für das Eigenschaftspaar normale—*unifoliata*-Blätter, *Uni—uni*, und eines für die Umbildung der Blütenelemente in grüne Blättchen, teils dass diese beiden konstatierten Haupteigenschaften der Mutante rezessive Charaktere darstellen.

Anschliessend an vorstehende Besprechung einer Mutante von *Ph. multiflorus* sei eine von RIESER i. c. gemachte Angabe über *Ph. angu-*

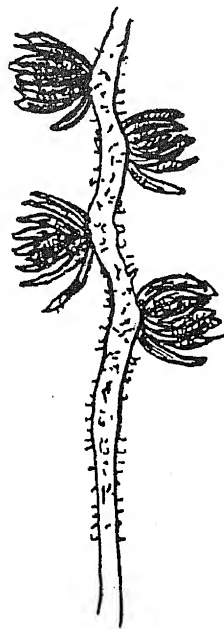


Fig. 7. (= RIESERS Fig. XV). Teil einer sterilen Infloreszenz der *unifoliata*-Mutation von *Ph. multiflorus* (dessin d'après nature).



*laris* zitiert. Er schreibt: »A. F. BLAKESLEE (1919) a trouvé dans une population de 450000 plantes de haricots »Adzuki« (*Phaseolus angularis*) un exemplaire unifoliolée; cet exemplaire comme le nôtre s'est montré complètement stérile. Déjà précédemment, on avait trouvé une mutation semblable chez trois exemplaires de *Phaseolus vulgaris*». Es scheint also auch bei *Ph. angularis* eine Komplexmutation konstatiert worden zu sein, an der zwei Genpaare beteiligt sind, das eine für das Eigenschaftspaar normale—*unifoliata*-Blätter, das andere für eine Umbildung von Blütenelementen. Ein Studium der Originalangaben ist mir leider nicht möglich gewesen, da das betreffende Zitat RIESERS in bezug auf die Publikationsstelle fehlerhaft zu sein scheint; in Botanical

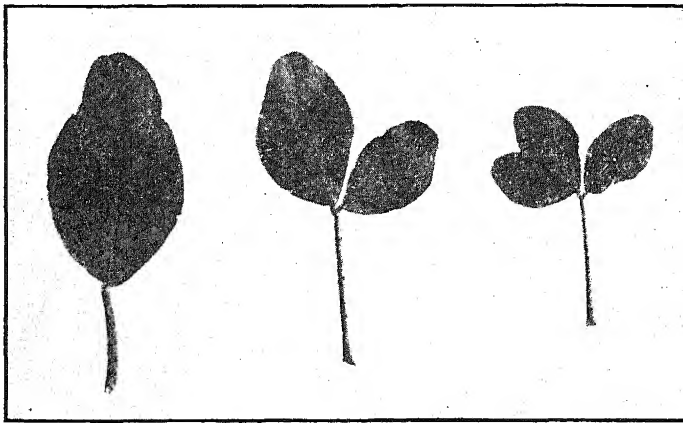


Fig. 8. Blatttypen von *unifoliata*-Pflanzen von *Pisum sativum*.

Abstracts 1919 findet sich keine Arbeit von BLAKESLEE, die etwas über *Ph. angularis* enthält.

Über eine Mutante von *Pisum sativum*, die in mehreren Hinsichten analoge Erscheinungen mit den vorhin für *Phaseolus vulgaris* und *multiflorus* beschriebenen (und wohl auch *angularis*) aufweist, habe ich früher in zwei Arbeiten (LAMPRECHT 1933 a und b) berichtet. Diese Mutante weicht von den normalen Formen von *Pisum sativum* in drei Hinsichten ab: 1. im Bau der Blätter, 2. durch die wiederholt verzweigte Infloreszenz und 3. in bezug auf die Blütenelemente.

Die Blätter zeigen *unifoliata*-Typus, analog dem, der vorhin für meine *unifoliata*-Mutante von *Phaseolus vulgaris* und für RIESERS Mutante von *Ph. multiflorus* beschrieben worden ist. Es treten also auch bei *Pisum* nicht nur einfache sondern überdies zwei- und dreiteilige

Blätter auf, und zwar stets auf ein und derselben Pflanze. Drei solche Blatttypen sind in Fig. 8 dargestellt.

Die Infloreszenzen des in Rede stehenden *unifoliata*-Typus von *Pisum* zeigen, mit zunehmend kürzer werdenden Abständen, wiederholte Verzweigungen. Die Verzweigungspunkte liegen so dicht, dass ein köpfchenartiges Gebilde entsteht. Zwei solche »Blütenstände« sind in Fig. 9 abgebildet. Die Art der Verzweigung ist wegen der Dichte derselben und der verhältnismässig dicken Blütenstiele schwer sicher festzustellen, gleicht aber am ehesten einer Trugdolde.

Die Blüten sind in allen ihren Teilen stark umgebildet. Sie bestehen ausschliesslich aus kleinen grünen Blättchen mit mehr oder weniger

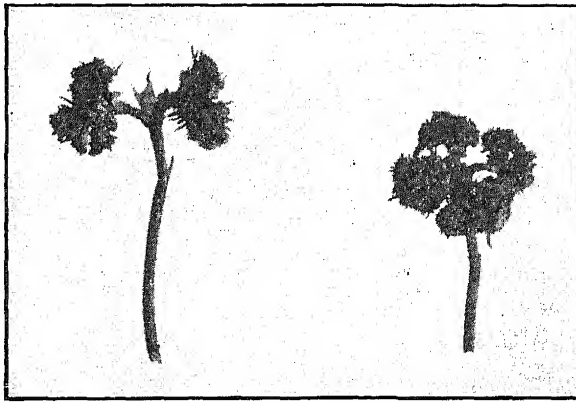


Fig. 9. Reich verzweigte und pistilloid umgebildete Infloreszenzen von *Pisum sativum* von köpfchenähnlichem Aussehen.

stark ausgebildeter Pistilloidie. Auch auf den spitzen, schmalen Blättchen, die in der Fig. 9 aus den Köpfchen ein wenig vorragen, und die auf Grund ihrer Stellung offenbar den Kelchblättern entsprechen, findet man am Rande gewöhnlich eine oder mehrere Samenanlagen.

Die Vererbung dieser *unifoliata*-Form ist von mir bisher in spaltenden Familien von zusammen etwa 3,000 Individuen untersucht worden. Hierbei hat durchweg eine monohybride Spaltung nach dem Verhältnisse 3 normale : 1 *unifoliata*-Pflanzen festgestellt werden können. Es hatte demnach immer den Anschein, als ob die oben erwähnten drei Abnormitäten durch nur ein Genpaar (*Uni—uni*) bedingt würden. Wie schon früher (LAMPRECHT 1933 a) hervorgehoben worden ist, könnte es sich um drei sehr stark gekoppelte Gene handeln. Da unter etwa 3,000 Individuen bisher keine Umkombination der erwähnten

Eigenschaften hat festgestellt werden können, so müsste der Crossing-over-Prozent solchenfalls weniger als 1 % betragen.

In meiner zweiten Arbeit über die Vererbung dieses *unifoliata*-Typus (LAMPRECHT 1933 b) ist nachgewiesen worden, dass das Gen *Uni* teils stark mit dem Gen *M* für Marmorierung der Samenschale gekoppelt ist und teils dass es zusammen mit diesem in unmittelbarer Nähe des Endes des *B*-Chromosoms liegt. Im Zusammenhang mit dieser Feststellung ist i. c. auch die Möglichkeit in Betracht gezogen worden, dass die gefundene Spaltung rein chromosomal bedingt sein könnte, verursacht z. B. durch den Wegfall eines kleinen Stückes am Endes des *B*-Chromosoms, das solchenfalls die betreffenden Gene enthalten müsste. Diese letztgenannte Möglichkeit halte ich nunmehr für weniger wahrscheinlich. Auf andere interchromosomale Ursachen zur Erklärung der besprochenen Erscheinungen wird im folgenden — bei Berücksichtigung des für alle drei bzw. vier Arten bekanntgewordenen Tatsachenmaterials — eingegangen werden.

Um bei der folgenden Diskussion einen besseren Überblick über das besprochene Mutationsmaterial zu bekommen, sind die wichtigsten Daten für dasselbe in Tabelle 1 zusammengestellt.

Wie ersichtlich, sind in Tabelle 1 sechs Mutationen aufgenommen, die alle durch *unifoliata*-Blätter charakterisiert sind. Diese Mutationen verteilen sich auf vier verschiedene Arten, nämlich auf drei *Phaseolus*-Arten und *Pisum sativum*. Von diesen sechs *unifoliata*-Mutationen sind zwei fertil, mit normal gebauten Blüten und Infloreszenzen, während die übrigen vier vollkommen steril sind und gleichzeitig auch mehr oder weniger stark umgebildete Blütenelemente aufweisen. Zwei von den letzteren Mutationen haben ausserdem verzweigte Infloreszenzen.

In bezug auf ihre Vererbung sind von den angeführten Eigenschaften für sich zwei, der *unifoliata*-Blatttypus und die Verzweigung der Infloreszenz, und zwar beide bei *Phaseolus vulgaris* studiert worden. Beide haben sich als genetisch einfach rezessiv bedingte Eigenschaften herausgestellt, den Genpaaren *Uni—uni* und *Ram—ram* entsprechend. Das Genpaar *Uni—uni* scheint für die besprochenen Mutationen wenigstens dreier Arten, nämlich *Ph. vulgaris*, *multiflorus* und *Pisum sativum*, mit Recht als homolog bezeichnet werden zu können. In bezug auf *Ph. angularis* sind die Angaben ungenügend um nähere Schlüsse ziehen zu können. Bei *Ph. vulgaris* und *multiflorus* haben die *unifoliata*-Blätter, wie ich früher nachgewiesen habe, ganz gleichen Bau, was

übrigens auch für *Pisum sativum* gilt, wenn von dem Fehlen von Stipellen und der Form der Teilblättchen abgesehen wird. Diesbezüglich muss man indessen eingedenk sein, dass der Phänotypus stets von der Gesamtgenenkonstitution bestimmt wird; für die Abweichungen werden hier also andere Gene verantwortlich sein.

TABELLE 1. Übersicht über das Mutationsmaterial.

Pflanzenart	Mutante beschrieben von	Blätter	Infloreszenzen	Blüten	Anmerkung
<i>Phaseolus vulgaris</i>	LAMPRECHT 1935 b	<i>unifoliata</i>	normal (nicht verzweigt)	fertil	Aus der Sorte Favorit
»	LAMPRECHT in vorliegender Arbeit	<i>unifoliata</i>	normal (nicht verzweigt)	fertil	Aus der Sorte Hundert für Eine
»	LAMPRECHT in vorliegender Arbeit	<i>unifoliata</i>	verzweigt	steril	Blütenelemente teilweise missbildet; mit 3 Fruchtblättern
<i>Phaseolus multiflorus</i>	D. RIESER 1924	<i>unifoliata</i>	normal (nicht verzweigt)	steril	Blütenelemente durchweg phylloid umgebildet
<i>Phaseolus angularis</i>	A. BLAKESLEE 1919? (zitiert nach RIESER 1924)	<i>unifoliata</i>	?	steril	Art der Umbildung von Blütenelementen nicht erwähnt
<i>Pisum sativum</i>	LAMPRECHT 1933 a	<i>unifoliata</i>	verzweigt	steril	Blütenelemente durchweg pistilloid umgebildet

Gleiches wird offenbar auch für die Verzweigung der Infloreszenzen Gültigkeit haben. Auch hier dürfte es sich bei *Ph. vulgaris* und *Pisum sativum* um dasselbe Genpaar *Ram—ram* handeln. Für *Ph. vulgaris* liegt, wie schon früher erwähnt worden ist, diesbezüglich eine umfangreiche genetische Analyse vor (LAMPRECHT 1935 a).

Schliesslich finden wir bei vier der Mutationen eine Umbildung von Blütenelementen, die in ihrer Beschaffenheit variiert, aber stets mit vollkommener Sterilität verknüpft ist. Für diese, hier genetisch

für sich bisher nicht analysierte Eigenschaft nehme ich ein hypothetisches Genpaar an und bezeichne dasselbe, abgeleitet von Sterilität, mit *Ste—ste*. Die bei den verschiedenen Mutanten verschiedene Umbildung von Blütenelementen dürfte sicherlich mit der übrigen genotypischen Konstitution der in Frage stehenden Art bzw. Form in Zusammenhang zu bringen sein. Ausgeschlossen scheint auch nicht, dass noch ein oder mehrere weitere Genpaare an der Mutation beteiligt sind.

Gestützt auf das vorgebrachte Tatsachenmaterial nehme ich an, dass es sich bei den angeführten vier sterilen Mutationen um *Komplexmutationen* handelt, die *wenigstens zwei bzw. drei homologe Genpaare* der in Frage stehenden Arten betreffen.

Diese Annahme soll indessen vor allem als Arbeitshypothese aufgefasst werden. Ein exakter Beweis dürfte aber mit dem zur Verfügung stehenden Material von *Ph. vulgaris* und *multiflorus* zweifellos erbracht werden können. Von *Ph. vulgaris* verfüge ich über Linien mit verzweigter und unverzweigter Infloreszenzachse (siehe LAMPRECHT 1935 a), über Linien vom *unifoliata*-Typus (siehe LAMPRECHT 1935 b) und schliesslich dürfte die anscheinend pollenfertile Mutante mit drei Fruchtblättern (weibchensteril) als ♂ verwendet werden können. Kreuzungen zwischen diesen Linien werden klarlegen ob und in welchem Grade die an den Mutationen beteiligten Genpaare gekoppelt sind. Gleiches wird wahrscheinlich auch für *Ph. multiflorus* ermittelt werden können, da aus Kreuzungen zwischen dieser Art und *Ph. vulgaris* niedrige, vollkommen fertile Linien mit *multiflorus*-Charakteren zur Verfügung stehen.

Dass wir es bei den vier sterilen Formen um gleichzeitige Mutationen in mehreren Genen, sogenannten Komplexmutationen zu tun haben, dürfte kaum zu bezweifeln sein. Die in Frage stehenden Gene sind dann wahrscheinlich stark gekoppelt. Welche können nun die *Ursachen eines gleichzeitigen Mutierens mehrerer Gene* sein? Höchst wahrscheinlich sind inter- oder intrachromosomale Verhältnisse entscheidend.

Als interchromosomale Ursache wäre an den schon früher erwähnten Wegfall eines Stückchens am Ende eines Chromosoms zu denken, das solchenfalls die betreffenden Gene enthalten müsste. In solchen Fällen wäre ein Crossing-over im betreffenden Chromosomenstück und damit auch eine Umkombination der dort liegenden Gene unmöglich. Also so wie die Verhältnisse bei der *Pisum*-Mutation sich bisher gezeigt haben.

Als intrachromosomale Ursache könnte die physikalisch-chemische

Beschaffenheit der betreffenden (benachbarten) Gene im Kolloidkörper des Chromosoms solcherart sein, dass die Bedingungen für eine Mutation für diese praktisch genommen gleich sind. Dann würden diese in der Regel eben gemeinsam mutieren. Diesfalls sollte ein Crossing-over stattfinden können. Aber auch hier erscheint eine vollkommene Unterdrückung des Crossing-over nicht ausgeschlossen, nämlich dann, wenn die Komplexmutation mit einem inversen Austausch des betreffenden Chromosomensegments verknüpft würde. Zwischen derartigen Chromosomensegmenten findet nämlich — soweit bisher bekannt — niemals ein Crossing-over statt. Auch auf diese Fragen wird durch Kreuzungsexperimente Antwort erhalten werden können.

### SUMMARY.

1. The author describes two new mutations in *Phaseolus vulgaris*, both characterized by entire leaves, so-called *unifoliata* type. At the same time reference is made to the published results of investigations of similar *unifoliata* types in *Phaseolus vulgaris* (LAMPRECHT 1935 b), *multiflorus* (RIESER 1924), *angularis* (BLAKESLEE 1919) and *Pisum sativum* (LAMPRECHT 1933 a and b).

2. It appears that among the six *unifoliata* mutations examined not less than four are sterile with more or less highly transformed floral parts. Two of the latter have besides branched inflorescences.

3. In *Ph. vulgaris* lines with only *unifoliata* leaves and only branched inflorescences are known and also genetically examined. Both the characters in question are singly recessive, corresponding to the gene pairs *Uni—uni* and *Ram—ram*.

4. In the *unifoliata* type of *Pisum sativum* the three characters *unifoliata* leaves, branched inflorescences and sterile, transformed floral parts are however *apparently* transmitted together as a single recessive.

5. As a mutation has now been demonstrated in *Ph. vulgaris*, which likewise encountered at the same time the three characters of *Pisum* mentioned, and as with respect to at least two of these characters a similar mutation has been shown by RIESER in *Ph. multiflorus* and by BLAKESLEE in *Ph. angularis*, it is therefore assumed that in the cases referred to we have complex mutations of homologous genes, which are probably closely linked.

6. Finally, the possibility is discussed of proving exactly the working hypothesis laid down by crosses between the lines available

in the material of *Ph. vulgaris*, which seems in all probability to be practicable.

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# CYTOLOGICAL STUDIES IN ALLIUM, VI THE CHROMOSOME MORPHOLOGY OF SOME DIPLOID SPECIES OF ALLIUM

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THE present paper is intended as a continuation of an earlier work (LEVAN, 1932), dealing with the chromosome morphology of a number of *Allium* species having a number of chromosomes deviating from the 8 series. The greater part of the present work, on the other hand, will deal with species of *Allium* having 16 chromosomes, but some information will also be given concerning some cytologically imperfectly known species with 14 or 18 chromosomes. In most of the species a short descriptive account of meiosis is also given. A case of amphibivalent formation in a species with 16 chromosomes will be described more in detail.

The taxonomy of *Allium* is unfortunately rather incompletely known, the latest monographic treatment of the genus (REGEL, 1875) was published more than half a century ago and is therefore in many respects out of date. For this reason the control determination of *Allium* species is difficult. With respect to the majority of the species dealt with in this paper, I have, however, succeeded in obtaining fairly reliable determinations; if there is any doubt as to the identity of a species I have called attention to it in each separate case, and I have also tried to facilitate subsequent control by providing an illustration of the plant in question. The majority of the species mentioned are in culture at Hilleshög and I hope to be in a position later on to bestow more attention to the taxonomy of the family.

The cytological methods adopted in this investigation are on the whole the same as those employed in my previous *Allium* studies (LEVAN, 1932). Last summer I tried the fixation of pollen mother-cells in acetic acid alcohol and staining in warm aceto-carmin solution, which has been used so successfully, for instance, in the study of maize chromosomes, but the results as far as *Allium* is concerned were not as satisfactory as the NAVASHIN fixations.

The morphology of the somatic chromosomes has been studied in the first post-meiotic division in the pollen grain. I have attached



special importance to the production of all slides in exactly the same manner so that any differences in size between the chromosomes of different species can be regarded as significant. All pictures are drawn with the aid of the same system of lenses (ZEISS apochromatic immersion objective 1,5 mm + compensating ocular 12 X), which gives a magnification of about 3600 times. In the reproduction the pictures have been reduced to  $\frac{2}{3}$  of their original size.

As the chromosomes in the first pollen division are often situated in one plane, I have made a number of measurements of the lengths of the chromosomes. These measurements all refer to the metaphase stage. The measurement data must of course be treated with caution, but on the whole I have found them to be reliable.

With regard to the treatment of the various species in the following special section the arrangement adopted for each species is as follows:

1. *Material*. Garden material has been used almost exclusively. When only the name of a city is given this denotes that the material has been obtained from an official botanical garden in that city. »VAN TUBERGEN» signifies that the plants were purchased from the firm of VAN TUBERGEN, Haarlem, Holland.

2. *Somatic chromosomes*.

a) *Chromosome form*. The following types are distinguished. Medianly inserted chromosomes, the insertion constriction dividing the chromosome into parts less asymmetrical than 2 : 3.

Asymmetrical chromosomes, the two chromosome arms showing a greater asymmetry than 2 : 3.

Subterminally—terminally inserted chromosomes, the shorter arm being less than  $\frac{1}{4}$  of the entire chromosome.

In estimating the length of the chromosome arms the satellites or their attachment threads are not included. Chromosomes furnished with a satellite are generally named  $s_1$ ,  $s_2$ , etc., subterminally inserted chromosomes without any satellite  $st_1$ ,  $st_2$ , and terminally inserted chromosomes  $t_1$ ,  $t_2$ , but this has no reference to any possible chromosome homologies between the different species.

b) *Size of chromosomes*. 2 measurements are generally given, one for the smallest chromosome in the idiogram, provided it is not  $s$ ,  $st$  or  $t$ , and one for the largest. Further, the proportions are given for any possibly occurring  $s$ ,  $st$  and  $t$  chromosomes, these measurements being specified in the following order: longer arm + shorter arm + + attachment thread of satellite + satellite.

3. *Meiosis*, which is mostly described simply qualitatively. In

certain more extreme cases some information is supplied concerning the occurrence of chiasmata.

In this work, as in my previous investigations, my thanks are due to Dr. A. HÅKANSSON for most valuable advice and criticism.

## SPECIAL SECTION.

### I. SPECIES WITH 14 CHROMOSOMES.

Species with 14 chromosomes are *A. Allegheniense* SMALL, *Moly* L., *narcissiflorum* VILL., *stellatum* FRAS., and *ursinum* L. The somatic chromosomes of these species have already been described (*A. stellatum* by ANDERSON in 1931). Meiosis in *A. ursinum* has been investigated by CHODAT (1925) and meiosis in *A. Allegheniense* has been treated in my work mentioned above.

#### 1. *A. cernuum* ROTH.

*Material:* Gothenburg, Copenhagen, Munich. This species (Fig. 1) is very similar to *A. Allegheniense*, already described, but differs from that species in the shape of the petals. This form has already been examined cytologically by MOTTIER and NOTHNAGEL (1913), who, however, gave the chromosome number at  $n=8$ .

*Somatic chromosomes:* The haploid chromosome set of the species may be seen in Fig. 2 a. All chromosomes have median insertion. One chromosome furnished with a satellite ( $s_1$ ) is present.

*Size of chromosomes:*  $10-12 \mu$ .  $s_1 : 6,3 \pm 5,0 \mu$ .

Generally speaking it may be said that this karyotype is entirely in accord with the state of things in *A. Allegheniense*. The  $s_1$  chromosome

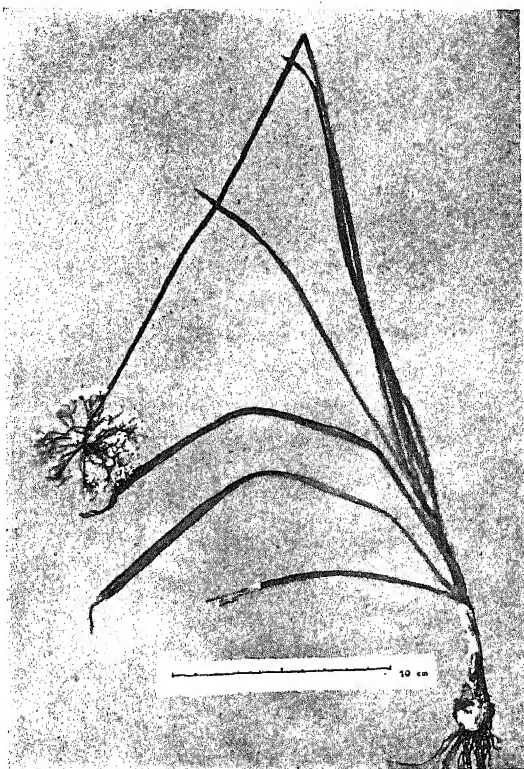


Fig. 1. *A. cernuum*.

is of the type predominant in the 14 chromosome species of *Allium*, the submedianly type with a small satellite attached to the shorter arm.

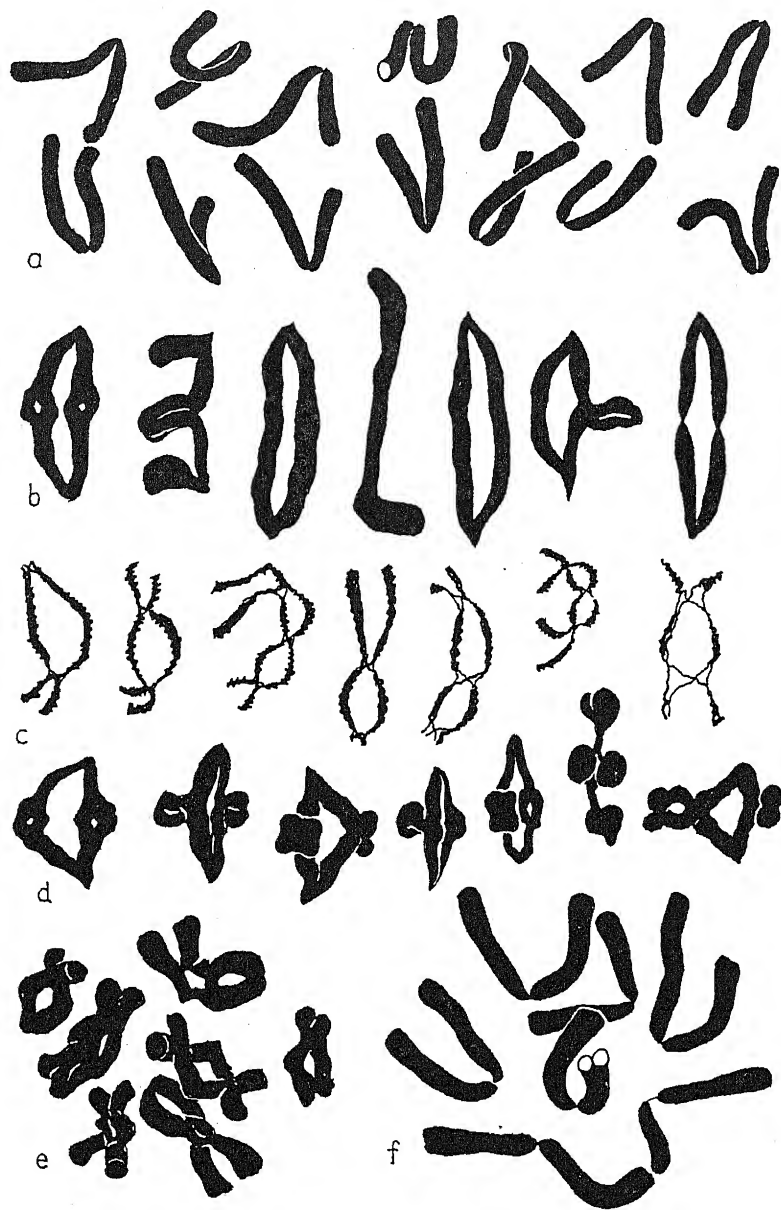


Fig. 2. *a—b*: *A. cernuum*, *a*: anaphase II, *b*: metaphase I, *c—e*: *A. narcissiflorum*, *c*: diakinesis, *d*: metaphase I, *e*: metaphase I in polar view, *f*: *A. neapolitanum*, first pollen metaphase. —  $\times 2400$ .

*Meiosis*: At metaphase I (Fig. 2 *b*) the plant examined (from Munich) is characterized by a terminalisation unusually high for *Allium*. A bivalent type, occurring frequently in this species but otherwise less common in *Allium*, is the ring form without any cross arms (Fig. 2 *b*, Nos. 3 and 5). Occasionally the places of association between the two chromosomes in the ring are drawn out into threads (Fig. 2 *b*, No. 7). There is however a great variation in the shape of the bivalent, thus, long side arms may occur but they seldom have more than 2 chiasmata per arm. The number of chiasmata found in 5 cells was the following:

No. of chiasmata	1	2	3	4	Tot. xx	Tot. term. xx	Term. coeff.
No. of cases .....	6	23	5	1	71	42	0,592

The terminalisation is considerably higher than in the examined form of *A. Allegheniense*.

## 2. *A. narcissiflorum* VILL.

*Material*: Copenhagen, VAN TUBERGEN.

*Meiosis*: To the pictures of somatic chromosomes already given (LEVAN, l. c.) I supplement a few pictures of diakinesis and metaphase I (Fig. 2 *c—e*). The terminalisation is considerably lower than in the preceding species. In 5 cells at metaphase I 84 chiasmata were counted, 13 of which were terminal (term. coeff. = 0,155).

## 3. *A. neapolitanum* CYR.

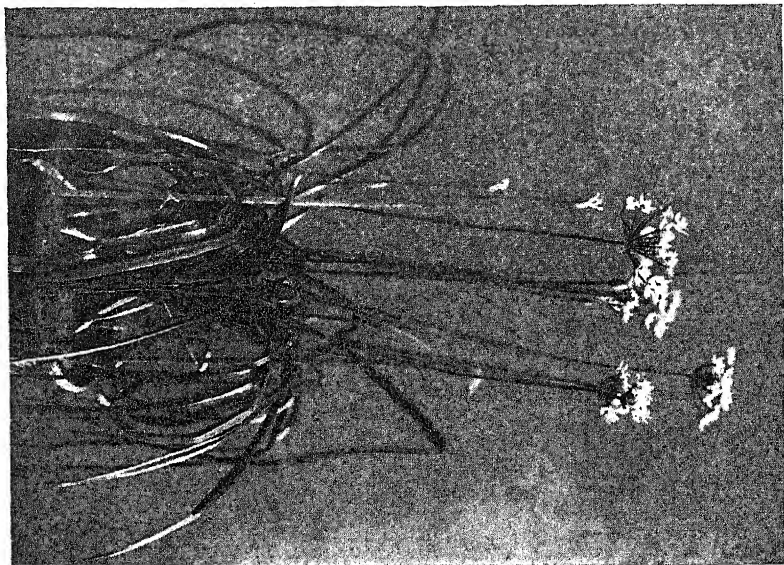
*Material*: Stockholm, VAN TUBERGEN.

*Somatic chromosomes*: In the Stockholm material, of which only root-tips were examined, I found the number  $2n = 28$ . But in the material from VAN TUBERGEN, raised in my cultures at Hilleshög (Fig. 3), the chromosome number was  $2n = 14$ . The chromosomes of the latter type all have median insertion (Fig. 2 *f*). No satellite chromosome could be detected.

*Size of chromosomes*: 11—15  $\mu$ .

## 4. *A. pendulinum* TEN.

*Material*: Copenhagen. Of this species I have examined 2 varieties, this 14-chromosome type from Copenhagen and another type with 18 chromosomes from VAN TUBERGEN, named *A. pendulum* (v. p. 316) in

Fig. 3. *A. neapolitanum*.Fig. 4. *A. pendulum* ( $n=7$ ).

this paper). The former type (Fig. 4) is a rather low plant with purely white flowers and is very much like *A. triquetrum*, to which species REGEL refers all forms of *A. pendulinum*. It has, however, quite a different idiogram from that of *A. triquetrum*. Both the 14- and the 18-chromosome types of *A. pendulinum* have sharp triangular stems with pendulous flowers.

*Somatic chromosomes:* In the pollen division the 14-chromosome type has 6 medianly and 1 ( $s_1$ ) subterminally inserted chromosomes, the  $s_1$  chromosome being furnished with a small satellite (Fig. 5 a).

*Size of chromosomes:* 8—13  $\mu$ .  $s_1$  : 7,0 + 1,0 + 0,8  $\mu$  (attachment thread).

## II. SPECIES WITH 16 CHROMOSOMES.

The great majority of *Allium* species have the somatic chromosome number of 16. Although a rather large number of 16-chromosome species of *Allium* have been investigated cytologically from time to time, there is, as far as I have been able to learn, very little exact information furnished with regard to the chromosome morphological constants, the position of the attachment constriction, the occurrence of satellites, etc. (In *A. Cepa* these particulars have been carefully described by TAYLOR, 1926.)

### 5. *A. albopilosum* WRIGHT.

*Material:* VAN TUBERGEN. This is a rather low plant with a large, luxuriant inflorescence (3 dm in diameter). The flowers are large with long, narrow, pointed petals.

*Somatic chromosomes:* 7 chromosomes have median insertion, one of them ( $s_1$ ) is plainly submedianly inserted and carries a small satellite on the shorter arm. In addition, there occurs a more asymmetric chromosome,  $s_2$ , which is also furnished with a satellite; the latter satellite has a somewhat longer attachment thread (Fig. 5 c, d).

*Size of chromosomes:* 7—11  $\mu$ .  $s_1$  : 4,3 + 3,3  $\mu$ .  $s_2$  : 5,0 + 2,0 + 1,2  $\mu$  (attachment thread).

*Meiosis:* In studying the prophase of meiosis in *A. albopilosum* I came across a condition in the nucleolus that merits description. Later on I shall recur to this matter when dealing with other species of *Allium*, where also some illustrations will be given (v. *A. Rosenbachianum*, Fig. 14 k—m).

At early leptotene there are 2 nucleoli in each cell, from pachytene there is only 1 and this disappears at late diakinesis. The interesting



Fig. 5. *a—b*: *A. pendulinum*, first pollen metaphase, *b*: 4 examples of  $s_1$ , *c—e*: *A. albobilosum*, *c—d*: first pollen metaphase, *d*:  $s_1$  and  $s_2$  from 4 plates, *e*: metaphase I, *f—g*: *A. amblyophyllum*, first pollen metaphase, *g*: 2 examples of  $s_1$ , *h—i*: *A. angulosum*, *j*: *A. nutans*, first pollen metaphase. —  $\times 2400$ .

point is that this nucleolus is evidently associated with a pair of chromosomes. The picture obtained of this state of things is the following: During pachytene—diplotene the nucleolus has one constriction dividing it into 2 parts, which may be either rather equal or unequal in size. A pair of chromosomes run to this constriction and the nucleolus is evidently attached to this chromosome pair. There is often an intensely coloured ring round the nucleolus in the constriction itself. Sometimes the chromosome pair continues on the other side of the constriction. This continuation may, however, be missing and in that case the attachment of the nucleolus to the chromosome pair will be terminal.

That the nucleolus is attached not only to a definite chromosome but also to a definite point of that chromosome can be plainly seen at the first pollen prophase in certain species of *Allium*, for instance, *A. Schoenoprasum*, where the nucleolus is attached to the  $s_1$  chromosome close to the satellite, or *A. zebdanense*, where the nucleolus is connected with the IX chromosome at the latter's insertion constriction.

Similar conditions in the nucleolus have been shown in quite a number of objects; the reader is referred to the works of HEITZ on the subject, in which *Allium* is also dealt with. In *Zea*, which is particularly well known in this respect (McCLINTOCK, 1931, and others), the nucleolus may exhibit the constriction commonly occurring in *Allium* (cf. for instance McCLINTOCK, l. c. Fig. 13, where the nucleolar parts marked by the constriction, however, show a greater difference in size than is usual in *Allium*). Also in *Agapanthus* the same condition of the nucleolus is found (DARLINGTON, 1933, Fig. 9, G).

At metaphase I in *A. albopilosum* (Fig. 5 c) there appear 20—25 chiasmata per cell, 4—7 of them being generally terminal.

#### 6. *A. amblyophyllum* KAR. et KIR.

*Material*: Lund.

*Somatic chromosomes*: 7 medianly and 1 ( $s_1$ ) subterminally attached, the  $s_1$  chromosome having a satellite (Fig. 5 f, g).

*Size of chromosomes*: 6—8  $\mu$ .  $s_1$ :  $4.5 + 1.0 + 0.7 + 1.5 \mu$ . The satellite is large,  $1.5 \mu$ , considerably longer than the shorter arm of the  $s_1$  chromosome.

#### 7. *A. ammophilum* HEUFF.

*Material*: Copenhagen. This species was fixed in Copenhagen in the summer of 1931. Unfortunately, it has not been possible to control the determination of the species. I have since, however, had several



similar types in culture, which have been determined as *A. angulosum* L.  $\delta$  *flavescens* REG., which is a synonym of *A. ammophilum* HEUFF. These other forms have, however, revealed other chromosome conditions. Most specimens examined hitherto are tetraploids ( $2n = 32$ ).

*Somatic chromosomes:* *A. ammophilum* from Copenhagen is however a diploid ( $2n = 16$ ). Unfortunately, its chromosome form has been studied only in the second meiotic division. All the 8 chromosomes show median insertion (Fig. 6 a, b). I am not in a position to express any opinion with regard to the occurrence of satellites, as satellites can be observed only in exceptional cases during meiosis.

*Size of chromosomes:* At second anaphase the chromosomes are  $6-9 \mu$  in length.

*Meiosis:* The characteristic feature of meiosis in this *Allium* form is the occurrence of an association of 4 chromosomes, an amphibivalent. The very clear prophase conditions in *Allium* have enabled me to follow this chromosome configuration from pachytene to anaphase I.

At pachytene we come across a striking feature. At a certain stage, when all the chromosomes are completely paired, there are always found in each cell a number of univalent threads (Fig. 6 c—i). These threads are plainly visible and easily recognized. Thus, they always show a lower degree of contraction than the surrounding paired threads and therefore the distance between their chromomeres is greater. As a rule, it is very difficult to follow these univalents for any distance, as they often pass right through the nucleus once or twice. But occasionally 2 of them can be seen to meet together and then continue paired (Fig. 6 f). In a few isolated cases I have succeeded in following the course of all four univalent threads in the nucleus of a cell and obtained pictures like that shown in Fig. 6 h. As seen, there is present here a typical quadrivalent configuration, but with that modification that the pairing region comprises only the ends of the 4 chromosomes.

In a later stage of pachytene these long univalent threads are not to be found. The pairing has advanced further and as a rule the only trace of the amphibivalent left is a cross at the point where the pairs of chromosomes exchange partners.

At diplotene, which in *Allium* often exhibits a large number of loops, all of which are certainly not enclosed by true chiasmata, the amphibivalent is more easily found (Fig. 6 j—m), and at diakinesis it begins to assume its definitive form (Fig. 6 n—q). All the 8 chromosome ends may be joined two and two together by means of chiasmata, then the amphibivalent assumes the form of a ring of four (Fig. 6 n, o), or

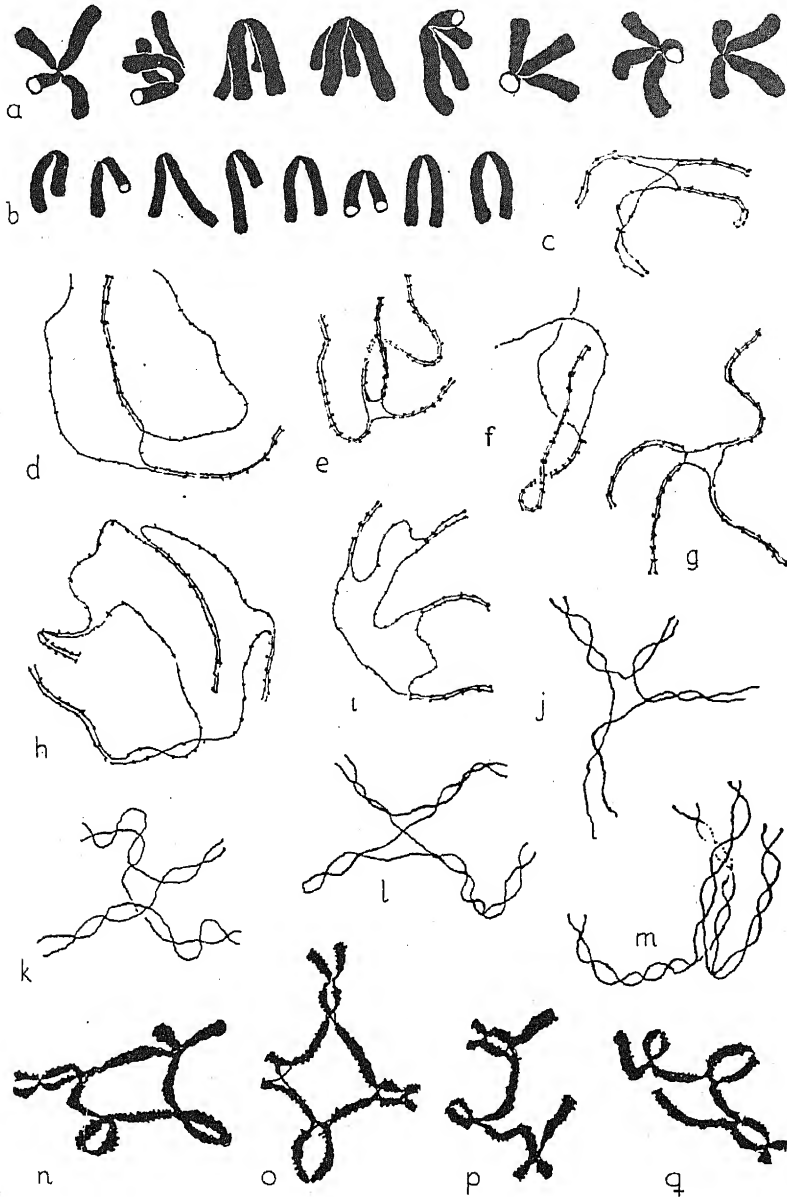


Fig. 6. *A. ammophilum*, a: metaphase II, b: anaphase II, c—q: the amphibivalent c—i: pachytene, j—m: diplotene, n—q: diakinesis. —  $\times 2400$ .

the pairing between two of the arms is lacking, when a chain of four is formed (Fig. 6 p, q). If 2 such pairings disappear without a

chiasmata being formed we get either a chain of three + a free univalent (Fig. 7 c) or 2 bivalents, which can never form rings.

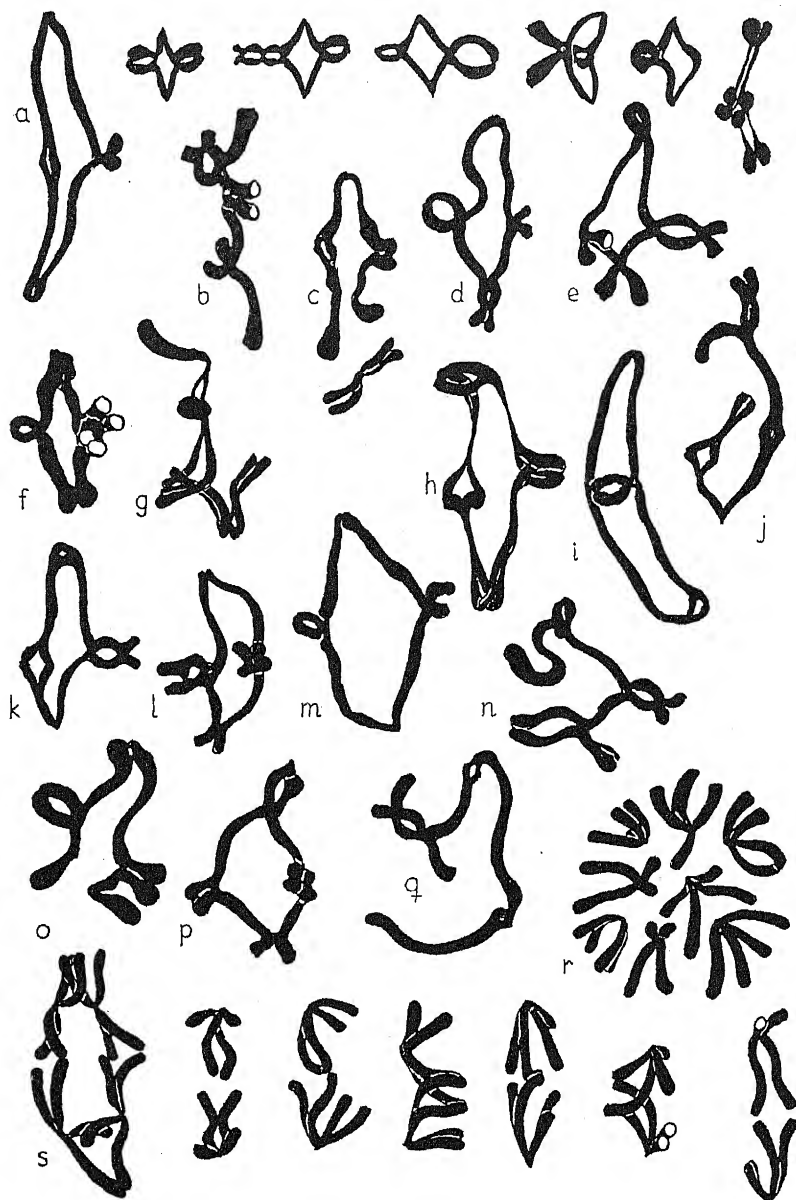


Fig. 7. *A. amnophilum*, a—q: metaphase I, a: the chromosome of one pollen mother cell, b—q: the amphibivalent, r—s: anaphase I, r: one anaphase plate in polar view, s: the chromosomes of one cell. —  $\times 2400$ .

At metaphase I the amphibivalent occurs in more than 80 per cent. of the cases. Of the amphibivalents previously described it mostly resembles the *Pisum* types (HÅKANSSON, 1931; RICHARDSON-SANSOME, 1932). The *Allium* amphibivalent has quite a large number of chiasmata. In some cases studied the following frequency of chiasmata was recorded:

No. of chiasmata	3	4	5	6	7	Tot. xx	xx: amphibival.
No. of cases .....	2	9	15	12	6	231	5.25

In the bivalents the frequency of chiasmata varies between 1 and 5 per bivalent, 2—3 being the number most frequently met with.

The form of the amphibivalent at metaphase I is most frequently a ring or a chain, the frequency of these two types being about equal (Fig. 7 *a—q*). Owing to the slight degree of terminalisation side arms or side rings are often formed. Of 95 chiasmata 24 were terminal (term coeff. 0.253). The appearance of the amphibivalent is more complicated than in species with greater terminalisation, for instance, *Campanula*, in which at metaphase only true rings and chains occur.

The position of the amphibivalent in the polar spindle is seldom zigzag, but generally the amphibivalent is orientated in such a manner that 2 adjacent chromosomes move to the same pole. The anaphase distributions observed are most frequently 8 + 8 (Fig. 7 *m*), although in occasional second divisions 7 + 9 chromosomes were observed in the both dyad nuclei. The separation at anaphase I can be actually observed (Fig. 7 *s*) and the chromatid arrangement reconstructed. Occasionally, vagabond univalents may be seen at first metaphase.

Unfortunately no later stages were fixed and therefore I am not in a position to investigate whether any semi-sterility is present.

#### 8. *A. angulosum* L. and 9. *A. nutans* L.

*Material:* Lund, Copenhagen, Leningrad. *A. angulosum* and *A. nutans* are two related species, differing from each other, among other features, in the length of the filaments. They constitute typical examples of polyploidy within the species. I have among my cultures forms with  $2n=16$  and forms with  $2n=>100$ , as well as a great many euploid and aneuploid chromosome numbers between these two extreme types. The cytology of these species will be made the subject of a special investigation on a subsequent occasion, but as typical

diploids occur within them I shall give some data here regarding their chromosomes.

*Somatic chromosomes:* The diploid *nutans* form from Lund, previously mentioned as  $L_{\text{subt}}$  (LEVAN, 1931), has all chromosomes medianly inserted. No satellite occurs (Fig. 5 j).

An *angulosum* form from Leningrad (my No. 149) has an exactly similar idiogram, with the exception that a typical  $s_1$  chromosome is present (Fig. 5 h).

A race of *angulosum* from Copenhagen has a similar idiogram; 8 medianly inserted chromosomes but without any satellite, there being also a small subterminally attached chromosome fragment (Fig. 5 i). In the plant examined this fragment occurs in about 30 per cent. of the pollen grains. It divides normally and behaves like a chromosome.

*Size of chromosomes:* 6—10  $\mu$ .  $s_1$  (in No. 149): 6,0 + 3,5  $\mu$ . The fragment: 2,0 + 0,9  $\mu$ .

#### 10. *A. azureum* BUNGE.

*Material:* Lund, Warsaw, VAN TUBERGEN. This widely cultivated ornamental bulb is evidently closely allied to *A. viviparum* KAR. et KIR., from which form it differs by its lacking of bulbils. *A. viviparum* is a polyploid.

*Somatic chromosomes:* *A. azureum* has 7 medianly inserted and 1 ( $s_1$ ) subterminally inserted chromosomes (Fig. 8 a). In the specimens from Lund and VAN TUBERGEN this  $s_1$  chromosome is furnished with a small satellite on its shorter arm; this subterminally inserted chromosome was also found in the Warsaw form but the satellite was missing (Fig. 8 b).

*Size of chromosomes:* 5—8  $\mu$ .  $s_1$ : 4,5 + 1,5  $\mu$ .

*Meiosis:* The meiotic course was normal. In metaphase I (Fig. 8 c) the bivalents have from 1 to 3 chiasmata. From 1 to 3 rod-shaped bivalents occur as a rule, the others form rings. The terminalisation coefficient for 5 cells was 0,280.

#### 11. *A. Farreri* STEARN.

*Material:* This species of *Allium* was kindly sent me by Mr. W. T. STEARN, London, who has described it taxonomically (STEARNS, 1930). It is very similar to other *Allium* forms which I have obtained by exchange of seeds from botanical gardens, for example, »*A. subangulatum*» from Kew, »*A. polyrhizum*» from Munich, and others, and



Fig. 8. a—c: *A. azureum*, a—b: first pollen metaphase, b: the asymmetric chromosome, c: metaphase I, d—h: *A. Farreri*, d—e: first pollen metaphase, e: the asymmetric chromosome, f: diakinesis, g—h: metaphase I, g: the bivalents of one cell. —  
 × 2400.

its cytology accords well with these forms. The appearance of the plant is seen in Fig. 9.

*Somatic chromosomes:* 7 of the chromosomes have median insertion while 1 is more asymmetric (Fig. 8 *d, e*). No satellite occurs. One or two secondary constrictions occur but not regularly.

*Size of chromosomes:* 7.5–10  $\mu$ . The asymmetric chromosome: 6.0 + 3.0  $\mu$ .

*Meiosis:* *A. Farreri* is a new example of chiasma localisation in meiosis. It behaves in the same manner as the previously described *A. fistulosum* (LEVAN, 1933 a). As in that species I have not been able to find any failure of pairing in *A. Farreri* at pachytene. In this case, however, I do not wish to express any definite opinion with regard to these early stages, as the fixations were not satisfactory.

As the chromosomes at diplotene form loops, the chiasmata appear to be arranged at random along the lengths of the chromosomes. Nor is any marked localisation apparent at early diakinesis (Fig. 8 *f*). At metaphase I, however, there is seen the strictly cruciform type of geminus, caused by 2



Fig. 9. *A. Farreri*.

chiasmata per bivalent, localized one on either side of the attachment constriction. In conformity with this there is always one cruciform bivalent in each cell furnished with arms of unequal length (Fig. 8 *g, h*).

## 12. *A. Cepa* L.

As I have not yet studied *A. Cepa* closely I will only mention that those forms I have examined — among them being the well-known commercial forms Zittauer and Braunschweiger, material from Wei-

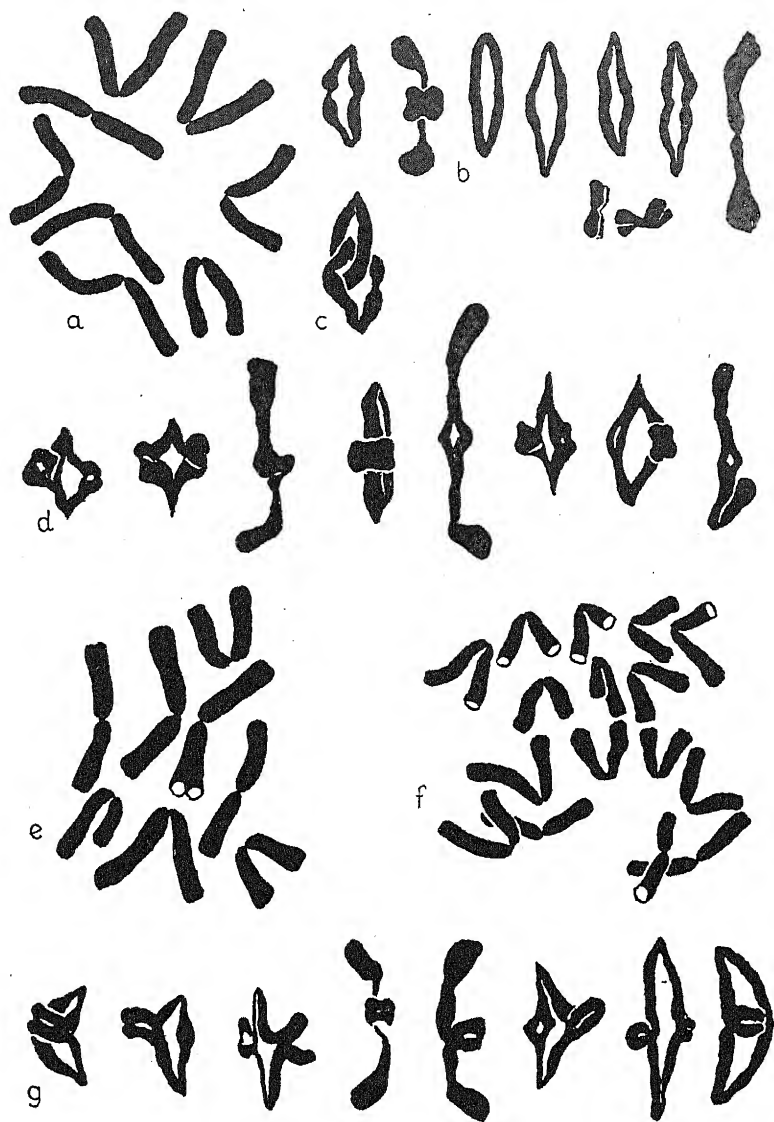


Fig. 10. a: *A. pulchellum*, first pollen metaphase, b—c: *A. flavum*, metaphase I, c: two interlocked bivalents, d: *A. paniculatum*, metaphase I, e—g: *A. Heldreichii*, e: first pollen metaphase, f: first pollen anaphase, g: metaphase I. —  $\times 2400$ .

bullsholm, Landskrona — show a random distribution of the chiasmata at first metaphase, in contradistinction to the related species *A. fistulosum*.



13. *A. flavum* L., 14. *A. paniculatum* L. and 15. *A. pulchellum* DON.

*Material:* VAN TUBERGEN, Lund, and other gardens. These three related species will be dealt with in another paper together with *A. carinatum* and *A. oleraceum*, and therefore the information given here is to be regarded as preliminary.

*Somatic chromosomes:* All forms have only medianly inserted chromosomes (Fig. 10 a). No

satellite occurs regularly. Sometimes, especially in certain forms of *A. flavum*, I have seen satellite-like formations, but they are to be regarded as incidental occurrences.

*Size of chromosomes:* 6—10  $\mu$ .

*Meiosis:* Conditions are similar in *A. paniculatum* and *A. pulchellum*. At metaphase I the number of chiasmata per cell is 16—20 with 5—7 terminal chiasmata (Fig. 10 d). On the other hand, the plant of *A. flavum* examined has at metaphase I an exceptionally high degree of terminalisation, in fact the highest ob-

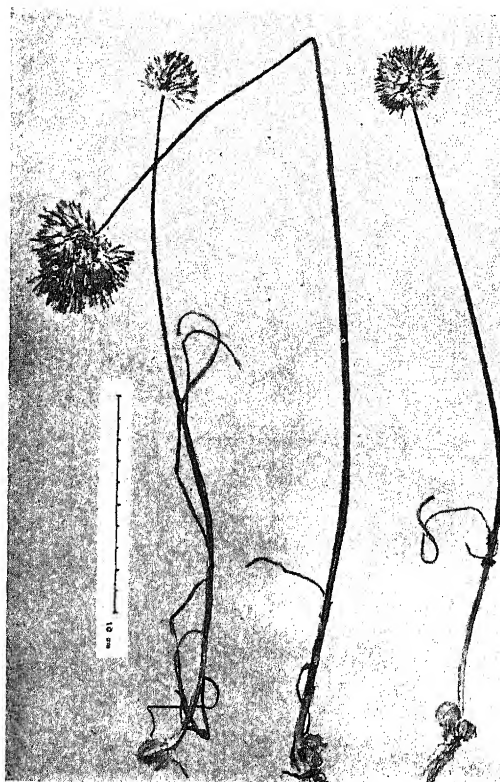


Fig. 11. *A. Heldreichii*.

served hitherto in *Allium*. Further, considerably fewer chiasmata occur than usual, 11—14 per cell, all of them, except one or two, being terminal (Fig. 10 b). Frequently 2 univalents are seen, the relative positions of which indicate that they have arisen by precocious separation of two chromosomes. All these facts suggest that in *A. flavum* the repulsive force localized in the spindle attachment is greater than is usually the case in *Allium*. Proximal interlocking is common in

*A. flavum* (Fig. 10 c). Perhaps this interlocking is a contributive cause of the anaphase disturbances frequently observed.

16. *A. Heldreichi* BOISS.

*Material*: Geneva, Toulouse. This species (Fig. 11) is similar to *A. Schoenoprasum*, but differs from that species in having thread-like lateral lobes in the filaments.

*Somatic chromosomes*: 8 medianly inserted chromosomes; no satellite is present. (Fig. 10 e, f).

*Size of chromosomes*: 7—11  $\mu$ .

*Meiosis*: The meiotic course is normal. At metaphase I (Fig. 10 g) there occur 1—3 rod-shaped bivalents.

17. *A. hymenorhizum* LEDEB.

*Material*: Lund, Copenhagen.

*Somatic chromosomes*: 7 medianly and 1 subterminally inserted, the latter ( $s_1$ ) furnished with a large satellite attached to the shorter arm by means of a long attachment thread (Fig. 12 a).

*Size of chromosomes*: 6—9  $\mu$ .  $s_1$ : 5,0 + 1,0 + 1,5 + 1,3  $\mu$ .

*Meiosis*: At metaphase I (Fig. 12 b) 8 ring-shaped bivalents are often formed, but usually 1 or 2 are shaped like rods. The following frequency of chiasmata was recorded in 5 cells:

No. of chiasmata	1	2	3	4	Tot. xx	Tot. term. xx	Term. coeff.
No. of cases .....	5	23	10	2	89	40	0,438

Interlocking of the proximal type occurred rather regularly (Fig. 12 b, d, e). Anaphase disturbances occur fairly frequently and sometimes chiasmata seem to resist the separation (Fig. 12 c).

18. *A. nigrum* L.

*Material*: VAN TUBERGEN.

*Somatic chromosomes*: 7 medianly inserted chromosomes and 1 asymmetric chromosome ( $s_1$ ) furnished with a small satellite (Fig. 12 f—g).

*Size of chromosomes*: 8—12  $\mu$ .  $s_1$ : 5 + 2  $\mu$ .

19. *A. obliquum* L.

*Material*: Lund.

*Somatic chromosomes*: 7 chromosomes with median insertion and 1 with subterminal insertion ( $s_1$ ), the latter furnished with a small satellite on a long attachment thread (Fig. 12 h, i).



Fig. 12. *a—e: A. hymenorhizum*, *a*: first pollen metaphase, *b*: metaphase I, *c*: anaphase I, *d—e*: 2 examples of interlocking, *f—g: A. nigrum*, first pollen metaphase, *g*: 4 examples of  $s_1$ , *h—j: A. obliquum*, *h—i*: first pollen metaphase, *i*: 5 examples of  $s_1$ , *j*: metaphase I, *k—n: A. Ostrowskianum*, *k—l*: first pollen metaphase, *l*: 4 examples of  $s_1$ , *m*: diplotene, showing the connection between one bivalent and the nucleolus, *n*: metaphase I. —  $\times 2400$ .

*Size of chromosomes:*  $5-9\ \mu$ .  $s_1: 5,0 + 1,5 + 2,0\ \mu$  + a small satellite.

*Meiosis:* At metaphase I all the 8 bivalents are formed into rings, but the  $s_1$  chromosome can still be recognized as it forms an asymmetric ring. The number of chiasmata is 18—20 per cell, with 9—10 terminal chiasmata (Fig. 12 j).

20. *A. Ostrowskianum*  
REG.

*Material:* Copenhagen, Lund (Fig. 13).

*Somatic chromosomes:* 7 medianly and 1 ( $s_1$ ) plainly submedianly inserted, the shorter arm of the latter having a rather large spherical satellite (Fig. 12 k, l).

*Size of chromosomes:*  $7-10\ \mu$ .  $s_1: 5,0 + 3,0 + 0,5 + 0,6\ \mu$ .

*Meiosis:* Early diplotene has a large number of loops. In this stage one chromosome pair is always associated with the nucleolus (Fig. 12 m)

in the same manner as that described above in *A. albopilosum*. At diakinesis—metaphase I there usually occur 2—3 chiasmata in each bivalent. With regard to the number of chiasmata in whole cells the following figures (the number of terminal chiasmata in the denominator) were found:

Diakinesis: 20/2, 18/1, 17/2.

Metaphase I: 19/9, 18/10, 16/7. (v. Fig. 12 n).

21. *A. Rosenbachianum* REG.

*Material:* VAN TUBERGEN. One red-flowered and one white-flowered type.



Fig. 13. *A. Ostrowskianum*.

Somatic chromosomes: 7 medianly inserted, 1 ( $s_1$ ) subterminally inserted and furnished with a satellite (Fig. 14 a, b).

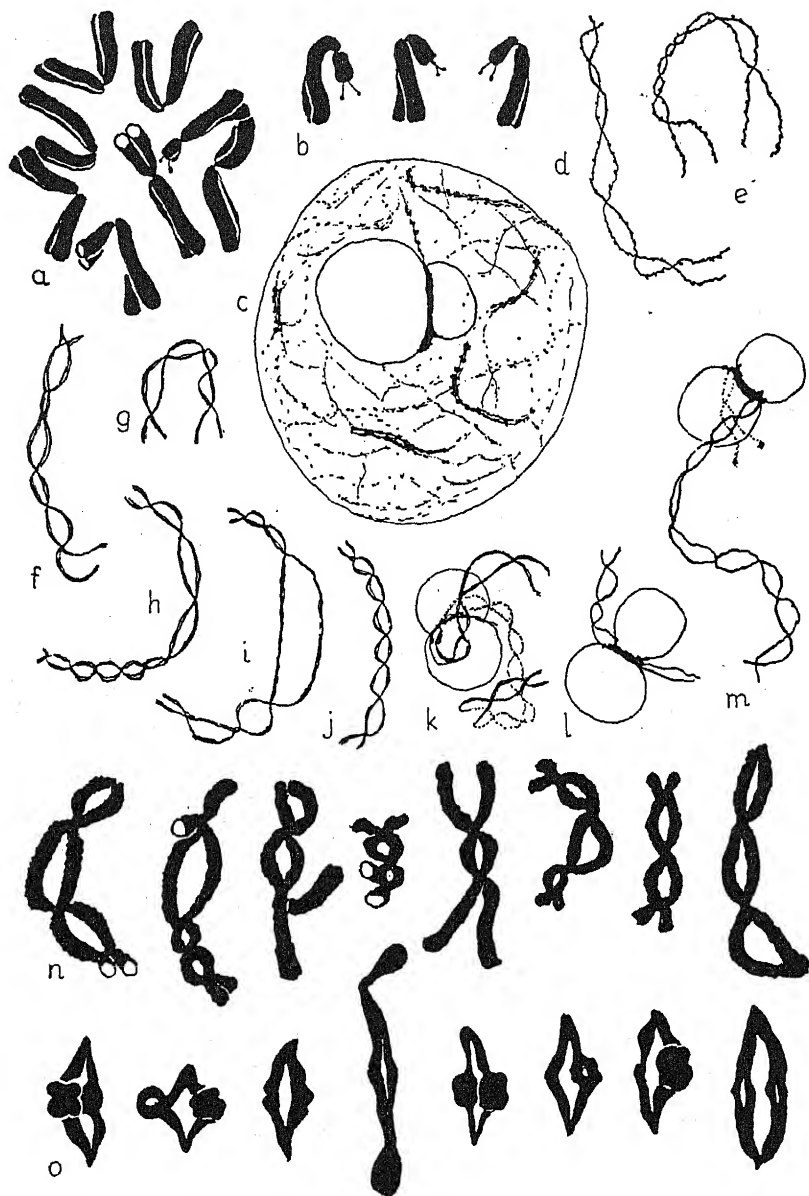


Fig. 14. *A. Rosenbachianum*, a—b: first pollen metaphase, b: 3 examples of  $s_1$ , c: zygotene, d—m: diplotene, k—m: the nucleolus bivalent, n: diakinesis, o: metaphase I. —  $\times 2400$ .

*Size of chromosomes:*  $8-10\mu$ .  $s_1 : 4,5 + 1,0 + 0,5\mu +$  a very small satellite.

*Meiosis:* This species was one of the most suitable for studying early prophase. Pairing at zygotene could be investigated. Already in that stage a connection was observed between one chromosome pair and the nucleolus (Fig. 14 c). The nucleolus showed the earlier mentioned constriction round the equator, which was intensely stained. This condition of the nucleolus could then be followed through pachytene and diplotene. In this latter stage the condition was very plain (Fig. 14 k—m) and the nucleolus does not appear to be terminally attached.

At diakinesis entire cells can be analysed, an example is shown in Fig. 14 n. The frequency of chiasmata in 5 cells during diakinesis was the following:

No. of chiasmata	1	2	3	4	5	Tot. xx	Tot. term. xx	Term. coeff.
No. of cases .....	1	6	18	14	1	128	17	0,133

At metaphase I the terminalisation has increased considerably (Fig. 14 o). No counts of chiasmata have been made at this stage.

22. *A. saxatile* RCHB. and 23. *A. Schoenoprasum* L.

*Material:* Lund and other botanical gardens. The determination of *A. saxatile* is uncertain. It resembles *A. Schoenoprasum* but differs from it, among other features, in having the stamina twice as long as the petals (Fig. 15). *A. Schoenoprasum* belongs to those species having polyploidy within the species. Its cytology will be treated in another connection. *A. saxatile* and the diploid *A. Schoenoprasum* agree with each other in their cytology.

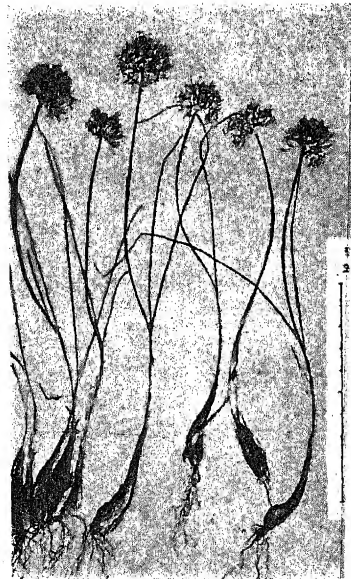


Fig. 15. *A. saxatile*.

*Somatic chromosomes:* Both species have 7 medianly attached chromosomes and 1 ( $s_1$ ) subterminally attached having a small satellite



Fig. 16. *a—c: A. saxatile*, *a—b*: first pollen metaphase, *b*: 4 examples of  $s_1$ , *c*: metaphase I, *d—f: A. scorodoprasmum*, *d—e*: first pollen metaphase, *e*:  $s_1$  and  $s_2$  from 2 plates, *f*: metaphase I, *g: A. sphaerocephalum*, first pollen metaphase, *h—i: A. stipitatum*, first pollen metaphase, *i*:  $s_1$ , *j—l: A. Suworowi*, first pollen metaphase, *k*: 5 examples of  $s_1$ , *l*: 5 examples of the long asymmetric chromosome. —  $\times 2400$ .

at its shorter arm, either on a long attachment thread or in poor fixation appearing as a small protuberance on the proximal arm of the chromosome (Fig. 16 a, b).

*Size of chromosomes:*  $5-7 \mu$ .  $s_1 : 4,5 + 0,5 \mu$ .

*Meiosis:* A picture is given of metaphase I in *A. saxatile* (Fig. 16 c), showing 6 ring-shaped and 2 rod-shaped bivalents, one of the latter being  $s_1$ .

#### 24. *A. scorodoprasum* L.

*Material:* Lund.

*Somatic chromosomes:* 6 chromosomes have median insertion, 2 chromosomes ( $s_1$  and  $s_2$ ) are subterminally inserted and both of them have a large satellite (Fig. 16 d, e). Owing to the difficulty of finding correct stages in the scanty flowered, bulbil-bearing inflorescences I have only examined one slide with pollen metaphases and therefore will not positively assert that both these s chromosomes are characteristic of the species. Certain pictures of the  $s_2$  chromosome convey the impression of a secondary constriction. In the flower examined both  $s_1$  and  $s_2$  occur however regularly.

*Size of chromosomes:*  $10-12 \mu$ .  $s_1 : 6,0 + 1,5 + 0,3 + 1,3 \mu$ .  $s_2 : 4,5 + 1,5 + 0,5 + 2,0 \mu$ .

*Meiosis:* Metaphase I shows a rather large number of chiasmata,  $21/5$ , in the cell reproduced (Fig. 16 f). The number of chiasmata per bivalent is 1—5. There is a great variation in the terminalisation.

#### 25. *A. sphaerocephalum* L.

*Material:* Lund.

*Somatic chromosomes:* 6 medianly inserted and 2 ( $s_1$  and  $s_2$ ) subterminally inserted having a long satellite (Fig. 16 g).

*Size of chromosomes:*  $6-8 \mu$ .  $s_1 : 3,0 + 1,0 + 1,5 \mu$  (the satellite).  $s_2 : 4,0 + 1,0 + 2,0 \mu$  (the satellite).

*Meiosis:* The meiotic course is normal. At metaphase I the terminalisation is rather high; the coefficient is about 0,5.

#### 26. *A. stipitatum* REG.

*Material:* VAN TUBERGEN.

*Somatic chromosomes:* 7 medianly inserted and 1 ( $s_1$ ) subterminally inserted and with a small satellite (Fig. 16 h, i).

*Size of chromosomes:*  $7-12 \mu$ .  $s_1 : 5,0 + 2,0 \mu$ .



27. *A. Suworowi* REG.

*Material:* Copenhagen.

*Somatic chromosomes:* 7 medianly inserted, one of which ( $l_1$ ) is evidently submedianly inserted. Besides, there is 1 chromosome ( $s_1$ ) with subterminal insertion and having a small satellite (Fig. 16 j—l).

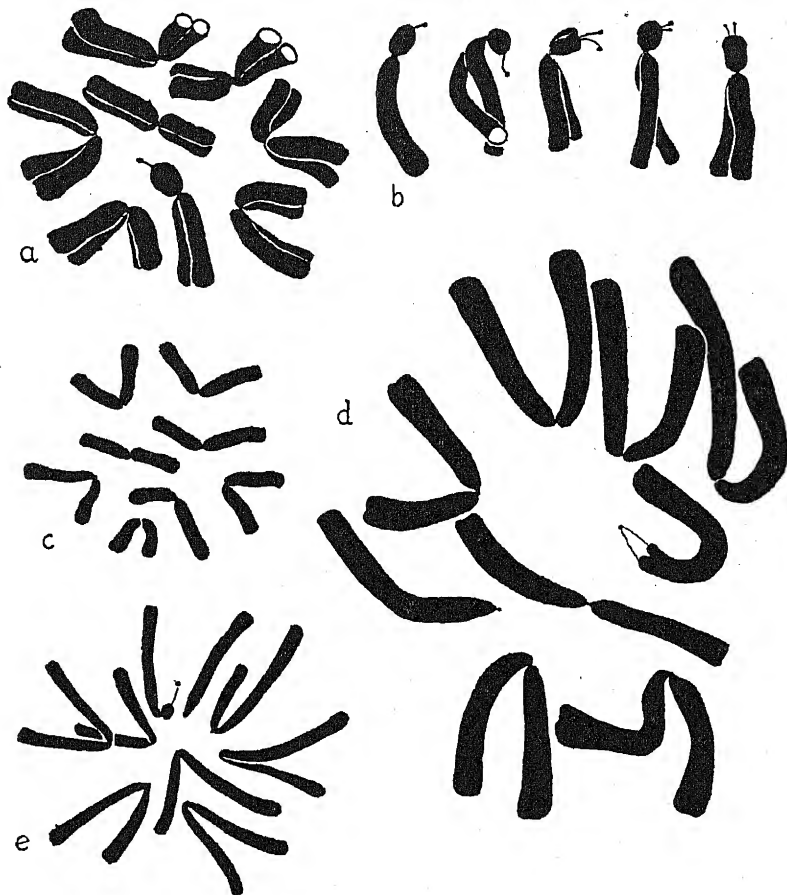


Fig. 17. a—b: *A. Victorialis*, first pollen metaphase, b: 5 examples of  $s_1$ , c: *A. yunnanense*, d: *A. fragrans*, first pollen metaphase, e: *A. pendulinum* ( $n=9$ ), first pollen anaphase. —  $\times 2400$ .

*Size of chromosomes:* 7—10  $\mu$ .  $l_1$ : 6,0 + 4,0  $\mu$ .  $s_1$ : 5,0 + 1,8  $\mu$ . The attachment thread of the satellite is often very long, up to 1,5  $\mu$ .

28. *A. Victorialis* L.

*Material:* Lund, Stockholm. The latter type was especially tall and stout. The cytology of both forms agreed, however, entirely. A

tetraploid form of this species has been recorded (HIRATA and AKIHAMA, 1927).

*Somatic chromosomes*: 7 medianly inserted and 1 ( $s_1$ ) subterminally inserted, the latter furnished with a small satellite (Fig. 17 a, b).

*Size of chromosomes*:  $6-10 \mu$ .  $s_1$ :  $6,0 + 1,8 \mu$  + an attachment thread which may reach  $1,5 \mu$  in length.

#### 29. *A. yunnanense* DIELS.

*Material*: Copenhagen, determination not checked.

*Somatic chromosomes*: All the 8 chromosomes are medianly inserted. No satellite occurred in the plant examined (Fig. 17 c).

*Chromosome size*:  $4-7 \mu$ .

30. *A. atropurpureum* WALDST. et KIT., 31. *A. giganteum* REG., 32. *A. magicum* L., 33. *A. sativum* L. and 34. *A. Schuberti* ZUEC.

*Material*: No. 33 from Lund, the others from VAN TUBERGEN. The cytology of these species has been studied as yet only in root mitoses. For that reason it has not been possible to investigate their chromosome morphology. All of them, however, have the chromosome number  $2n = 16$ .

### III. SPECIES WITH 18 CHROMOSOMES.

In *Allium* 2 species with 18 chromosomes have been described, viz. *A. karatawiense* and *A. triquetrum*. Besides, there is a species in the closely related genus *Nothoscordum*, i. e. *N. bivalve*, which also has 18 chromosomes. Below, are recorded 2 new 18-chromosome species of *Allium* and 1 new form of a *Nothoscordum* species.

#### 35. *A. (Nothoscordum) fragrans* L.

*Material*: Lund. This species has been investigated by KOERPERICH (1930), who found  $n = 8$ , all chromosomes having median insertion. The form I have examined has  $n = 9$  and the idiogram resembles that of *Nothoscordum bivalve* (ANDERSON, 1931).

*Somatic chromosomes*: 7 have median insertion, 2 ( $s_1$  and  $t$ ) have terminal insertion. One of the latter,  $s_1$ , has a very small proximal satellite (Fig. 17 d).

*Size of chromosomes*:  $13-22 \mu$ .  $s_1$ :  $10 \mu$ .  $t$ :  $11 \mu$ . The chromosomes of *A. fragrans* may be counted among the largest chromosomes known hitherto.

36. *A. pendulinum* TEN.

*Material:* VAN TUBERGEN. (v. No. 4, p. 295).

*Somatic chromosomes:* 7 medianly inserted, one chromosome ( $s_1$ ) having subterminal insertion and furnished with a small satellite; 1 chromosome ( $t_1$ ) is terminally inserted and has no satellite (Fig. 17 e).

*Size of chromosomes:* 8—14  $\mu$ .  $s_1$  : 5,5 + 1,0  $\mu$ .  $t_1$  : 6,5  $\mu$ .

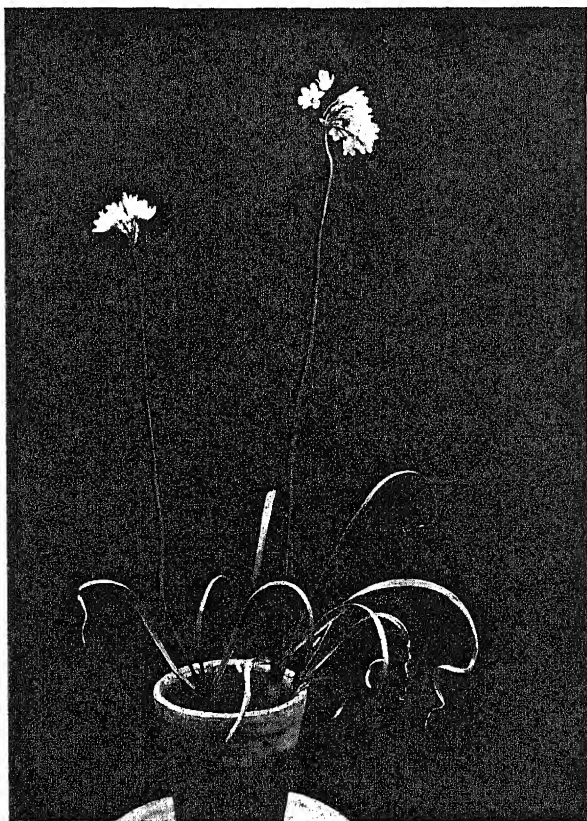


Fig. 18. *A. zebdanense*.

37. *A. zebdanense* BOISS. et NOE.

*Material:* Copenhagen. This species is a common ornamental plant, cultivated chiefly on account of its early flowering — in my cultures it can be seen in full bloom in the open air as early as the middle of March. The appearance of the plant can be seen from Fig. 18. It is allied to *A. triquetrum*, *A. pendulinum* and *A. neapolitanum*, but lacks the carina of the leaves of those species. The idiograms of these 4 species are also quite different.

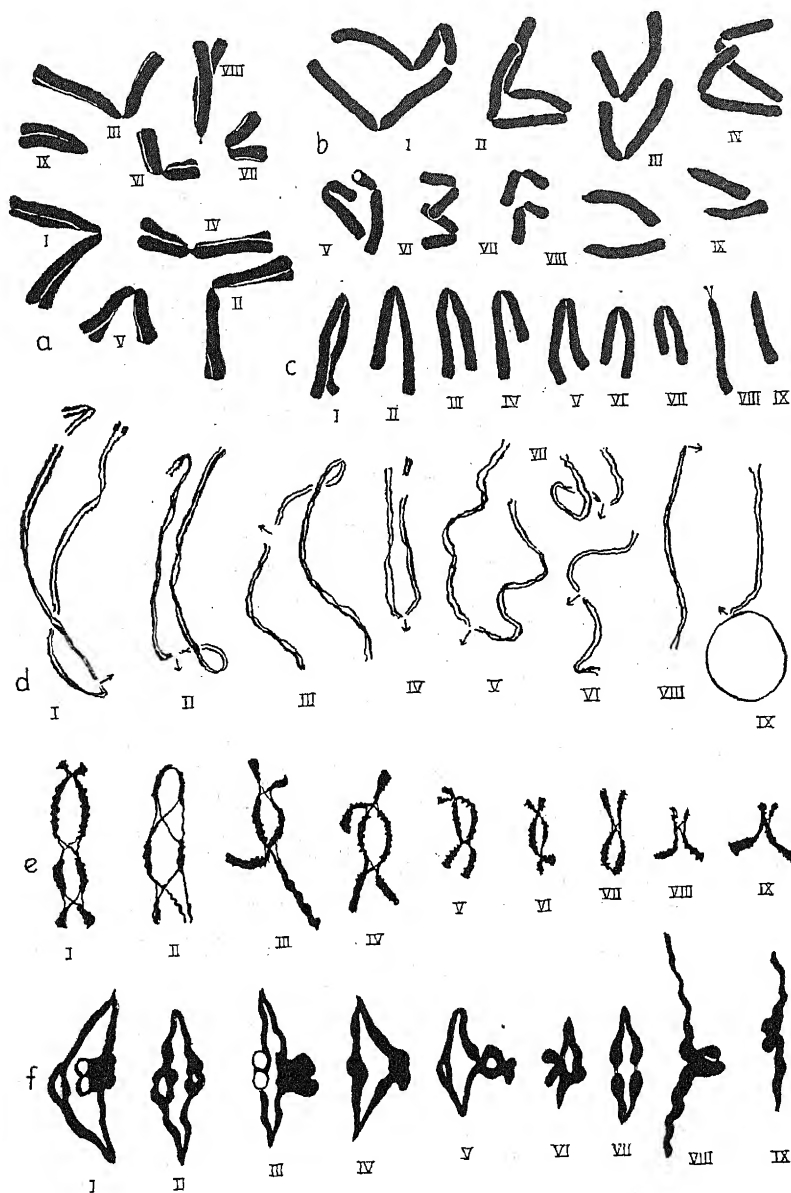


Fig. 19. *A. zebdanense*, a: first pollen metaphase, b: first pollen anaphase, c: anaphase II, d: first pollen prophase, e: diakinesis, f: metaphase I. —  $\times 2400$ .

*A. zebdanense* is in many respects an ideal cytological object. The fixations generally turn out exceedingly beautiful, even the various diakinetic stages, which are the most sensitive in fixing. The chromo-

somes are small in proportion to the cells, the pollen grains, for instance, are the largest known so far in diploid *Allium* species. All chromosomes can be identified not only in somatic divisions but also with some degree of certainty in meiosis.

According to WEBER (1929) [cited after TISCHLER, 1931] there is a form of *A. zebdanense* with  $n = 8$ . Those types I have studied have  $n = 9$ .

*Somatic chromosomes:* 7 of these chromosomes have median insertion while 2 have terminal insertion (Fig. 19 *a-c*). The former are denoted in order of size, beginning with the largest, I, II, III and so on up to VII, the 2 terminally inserted chromosomes are designated VIII, the larger, and IX, the smaller. VIII is furnished with an exceedingly small satellite, which is often difficult to detect. IX has in various stages shown itself to be connected to the nucleolus, which is attached to its proximal end.

The prophase of the first pollen division is very clear. All chromosomes can be identified (Fig. 19 *d*). The pole spindle attachments (marked in the Fig. with arrows) appear as gaps in the chromosomes, which gives the impression of fragmentation. Such achromatic bands are frequently observed also in other places within the chromosomes. They appear more regularly in 2 of the chromosomes, viz. I and IV. In both cases there is an achromatic band close to the end of the chromosome. These secondary constrictions can also be seen at diakinesis.

*Chromosome size:* In order to compare the chiasma frequency with the chromosome length present I thought it worth while to make careful measurements of all chromosomes in a number of pollen metaphases. The mean values obtained from 6 cells were the following:

Chromosomes	I	II	III	IV	V	VI	VII	VIII	IX
Long arm .....	5,3	4,7	5,1	4,5	3,6	2,6	2,5	5,2	4,0
Short arm .....	4,9	4,4	3,9	3,4	2,9	2,1	2,0	—	—
Total .....	10,2	9,1	9,0	7,9	6,6	4,7	4,5	5,2	4,0

*Meiosis:* The early stages of meiosis are of the usual type. From diakinesis onwards the different types of chromosomes can be identified (Fig. 19 *e*). The longest chromosomes, I to IV, have two or more chiasmata, the others have one or two. In entire cells we come across during diakinesis such numbers of chiasmata as 16/2, 18/1, 18/2, 19/3

and so on. The terminalisation coefficient of 10 cells at diakinesis was 0,135.

At metaphase I (Fig. 19 f) the bivalents I—VII most frequently form rings, the 2 smallest of them, VI and VII, however also assume the form of rods. The terminally inserted chromosomes VIII and IX always assume the shape of rods. Terminalisation is much greater

TABLE 1. *The chiasma frequency in A. zebdanense.*

Bivalent	Stage	Number of XX				Total term. XX	Total XX found	XX expect.	Term. coeff.
		1	2	3	4				
I	diakinesis .....	—	1	7	2	2	31	29,7	0,065
	metaphase I .....	—	5	2	3	15	28	30,7	0,536
II	diakinesis .....	—	5	5	—	3	25	26,5	0,120
	metaphase I .....	—	4	5	1	13	27	27,4	0,407
III	diakinesis .....	—	4	6	—	0	26	26,2	0,000
	metaphase I .....	—	4	6	—	13	26	27,1	0,500
IV	diakinesis .....	—	8	2	—	3	22	23,0	0,137
	metaphase I .....	—	5	5	—	14	25	23,8	0,560
V	diakinesis .....	—	10	—	—	4	20	19,2	0,200
	metaphase I .....	—	8	2	—	8	22	19,8	0,364
VI	diakinesis .....	3	7	—	—	6	17	13,7	0,353
	metaphase I .....	5	5	—	—	12	15	14,1	0,800
VII	diakinesis .....	7	3	—	—	3	13	13,1	0,231
	metaphase I .....	4	6	—	—	15	16	13,5	0,938
VIII	diakinesis .....	6	4	—	—	1	14	15,1	0,071
	metaphase I .....	5	5	—	—	7	15	15,6	0,467
IX	diakinesis .....	10	—	—	—	2	10	11,6	0,200
	metaphase I .....	10	—	—	—	5	10	12,0	0,500

than at diakinesis, the terminalisation coefficient obtained for 10 cells was 0,551.

In *A. zebdanense* it was possible to study the chiasma frequency of each bivalent separately. In Table 1 will be found data of the chiasma frequency in 10 cells at diakinesis and metaphase I, along with the values for each type of chromosome. In column 5 will be found the expected chiasma numbers for the chromosome length in question.

There is a rather good agreement between the expected numbers and the numbers found.

In the last column in Table 1 I have tabulated the terminalisation coefficients of the various classes of chromosomes. Although the material is much too small to permit of any definite conclusions being drawn, still, the tendency shown by these figures is interesting. Of the medianly inserted chromosomes the two shortest, VI and VII, have the highest degree of terminalisation. The two terminally inserted chromosomes, VIII and IX, have a considerably lower degree of terminalisation than might have been expected from their chromosome length. The location of spindle fibre attachment, however, is such that they should be compared, instead, with one of the arms of any of the longer chromosomes. Further, allowance must also be made for the fact that the same localized repulsion has a stronger effect within a ring than in free chromosome arms.

## GENERAL PART.

### I. FORM AND SIZE OF CHROMOSOMES.

In the following pages I shall endeavour to summarize the facts advanced in the preceding special part, and to find out whether they can furnish some assistance in arriving at more general conclusions with regard to the cytology of the genus. The first points that will be discussed are the form and size of the chromosomes.

The great majority of *Allium* chromosomes are of the 2-armed type with more or less median insertion. In several species the entire idiogram is built up of such chromosomes. However, there occur also a large number of aberrant chromosomes. Diagram 1 gives a picture of the proportions of a number of characteristic *Allium* chromosomes, which are characterized by the occurrence of satellites, by the characteristic location of the attachment or by both these attributes.

If the frequency of such aberrant types of chromosomes be put in relation with the chromosome numbers a striking feature will at once be apparent. Asymmetric chromosomes commonly occur in the 16- and 18-chromosome types but in the 8 known 14-chromosome types they are very rare. In fact, there occurs in them only 1 subterminally inserted chromosome, viz. the  $s_1$  in *A. pendulinum*. The 16-chromosome species have in the great majority of cases 1 plainly asymmetric chromosome while some have 2 such chromosomes. The following 16-chromosome species have median insertion in all the

chromosomes of the idiogram: *A. angulosum*—*nutans*, *Heldreichi*, *flavum*—*paniculatum*—*pulchellum* and *yunnanense*. Such idiograms

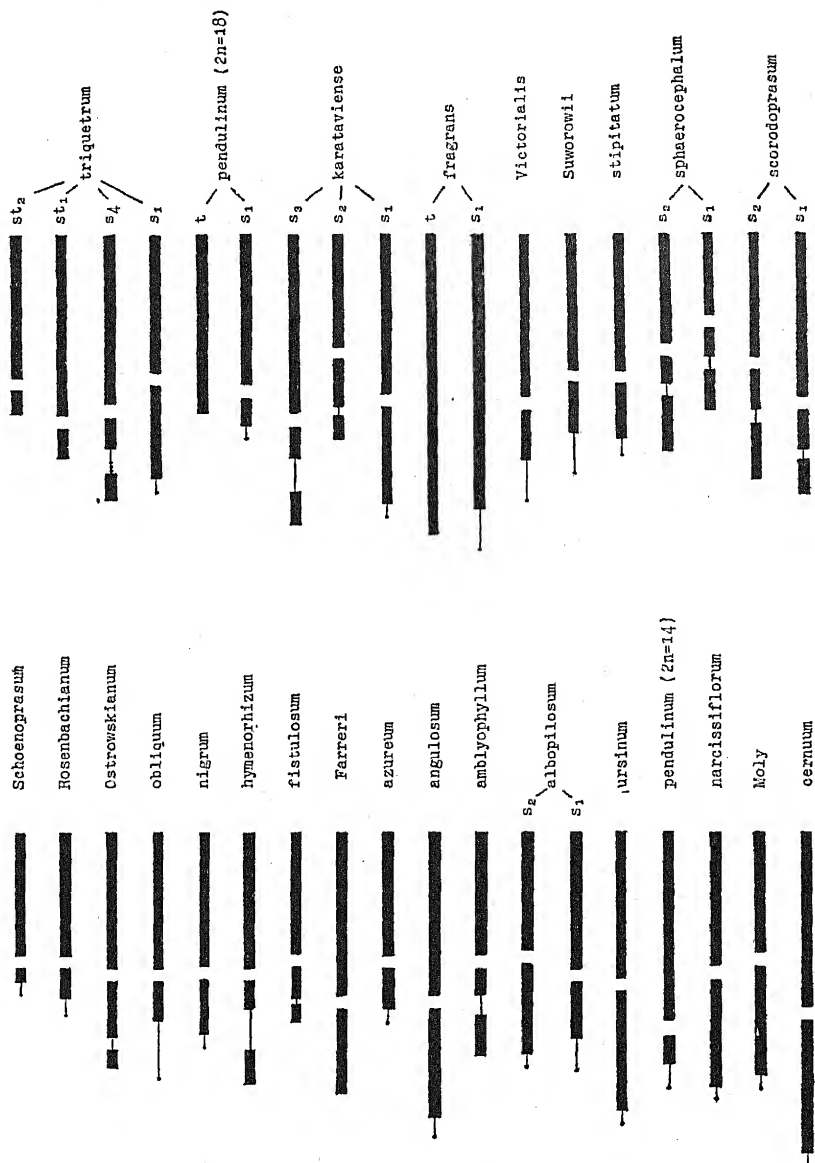


Diagram 1. The  $s_1$ ,  $st$  and  $t$  chromosomes from diploid *Allium* species. —  $\times 1800$ .

do not occur among the 18-chromosome species. Of the known 18 chromosome species 4 have the following haploid chromosomes 7 medianly inserted and 2 terminally or subterminally inserted. These



TABLE 2. *Proportions of chromosomes and pollen.*

Species	n =	Length of the longest chromosome	Chromosome width	Pollen length
<i>fragrans</i> .....	9	22	1,3	38,4
<i>neapolitanum</i> .....	7	15	1,1	—
<i>ursinum</i> .....	7	14	1,0	29,4
<i>pendulinum</i> .....	9	14	1,0	25,1
<i>Alleghehiense</i> .....	7	13	1,0	29,1
<i>cernuum</i> .....	7	13	1,0	—
<i>Moly</i> .....	7	13	1,0	30,0
<i>pendulinum</i> .....	7	13	0,9	29,8
<i>triquetrum</i> .....	9	13	1,0	30,6
<i>scorodoprasum</i> .....	8	12	1,3	22,5
<i>narcissiflorum</i> .....	7	11	1,0	28,4
<i>karataviense</i> .....	9	11	1,0	28,5
<i>albopilosum</i> .....	8	11	1,2	27,5
<i>zebdanense</i> .....	9	10	0,7	44,3
<i>Farreri</i> .....	8	10	1,2	26,3
<i>flavum</i> .....	8	10	0,9	32,7
<i>Ostrowskianum</i> .....	8	10	1,1	26,9
<i>paniculatum</i> .....	8	10	1,0	28,9
<i>pulchellum</i> .....	8	10	1,0	33,1
<i>Rosenbachianum</i> .....	8	10	0,9	26,8
<i>slipitatum</i> .....	8	10	1,0	27,5
<i>Suworowi</i> .....	8	10	1,0	30,0
<i>Victorialis</i> .....	8	10	1,3	30,1
<i>ammophilum</i> .....	8	9	0,9	—
<i>fistulosum</i> .....	8	9	0,9	31,0
<i>hymenorhizum</i> .....	8	9	0,8	26,8
<i>obliquum</i> .....	8	9	0,7	28,1
<i>amblyophyllum</i> .....	8	8	0,8	29,5
<i>azureum</i> .....	8	8	0,6	24,9
<i>sphaerocephalum</i> .....	8	8	0,8	31,5
<i>saxatile</i> .....	8	7	0,6	—
<i>Schoenoprasum</i> .....	8	7	0,6	24,6
<i>yunnanense</i> .....	8	7	0,7	31,2

4 species are *A. fragrans*, *karataviense*, *pendulinum* and *zebdanense*. The remaining species, *A. triquetrum*, has 3 subterminally inserted chromosomes.

As a rule there are no great variations in the size of the chromosomes within the same *Allium* idiogram. In species with 14 chromosomes in particular these differences in size are small, in general there

is only a difference of 2—3  $\mu$  between the largest and the smallest chromosome. Greater differences are found within the 16- and 18-chromosome species. For instance, in *A. triquetrum* and *A. zebdanense* the longest chromosome is more than twice the length of the shortest one.

On the other hand, there are considerable differences in the size of the chromosomes of the various species. In Table 2 the various species of *Allium* are arranged according to chromosome size, beginning with *A. fragrans* which has chromosomes 22  $\mu$  in length down to *A. Schoenoprasum* and *yunnanense* with chromosomes 7  $\mu$  in length. From this Table we obtain the following number of species in the various chromosome length classes:

Length in $\mu$	7	8	9	10	11	12	13	14	15—22	Average
No. of species .....	3	3	4	10	3	1	5	2	1—1	10,8 $\mu$

An interesting feature is the distribution of the different chromosome numbers in this tabular record. Above a limit of measurement between 12 and 13  $\mu$  we have:

6 species with 14 chromosomes  
 0 » » 16 »  
 3 » » 18 »

Below this limit there are:

1 species with 14 chromosomes  
 21 » » 16 »  
 2 » » 18 »

Thus, all the 16-chromosome species are situated below the limit of 12/13  $\mu$ . In other words, the average length of the longest chromosome

in 14-chromosome species is 13,1  $\mu$   
 » 16- » » » 9,2  $\mu$   
 » 18- » » » 14,0  $\mu$

The chromosome width in the different species is also given in Table 2. The measurements of width were made close to the insertion constriction during metaphase. Further towards the ends the chromosomes are often split and therefore measurements would give too great chromosome widths. The width of the chromosomes within an idio-

gram is constant, but in different idiograms the chromosome width is on the whole proportionate to the chromosome length so that the longer the chromosomes of the idiogram the greater the chromosome width. There are exceptions to this rule, but it cannot be determined whether they are due to possible varying contraction.

The occurrence of satellites in *Allium* is so frequent that it can be safely said that satellites constitute a characteristic feature of the *Allium* idiogram. A feature common for all satellite-bearing chromosomes in *Allium* is that the satellite is attached to the shorter arm of the chromosome.

Species in which no satellites at all occur are *A. neapolitanum*, *Farreri*, *flavum*—*paniculatum*—*pulchellum*, *Heldreichi* and *yunnanense*. Further, no satellites are found in certain diploid forms of *angulosum* and *nutans*, but in the polyploid forms of these two species satellite chromosomes are frequently met with.

The commonest form of satellite occurring in *Allium* is a very small ball considerably less in diameter than the chromosome itself. This type of satellite is the only one occurring in the 14-chromosome species known so far. It is also common in 16- and 18-chromosome forms but in these forms other types of satellites also occur, larger balls or entire rods. Such large satellites are found in the following species: *A. amblyophyllum*, *fistulosum*, *hymenorrhizum*, *Ostrowskianum*, *scorodoprasum*, *sphaerocephalum*, *karataviense* and *triquetrum*.

The length of the satellite attachment thread varies much between the different species. I have tried to obtain the correct proportions in Diagram 1. The length of the attachment thread, however, varies more than other characters owing to fixation also within the same species.

With regard to the metamorphoses that have taken place in the evolution of the present *Allium* idiograms some idea may be obtained by making a comparison between the different species. In this case the general principle holds good that differences in chromosome form, formation of satellite and the like must be regarded as due to structural changes within the idiogram, such as fragmentations and translocations, while variations in the size class of the chromosomes among the species must be considered as differences in the reaction of the chromosomes to the genotype (DARLINGTON, 1932).

Experiments in X ray radiation of *A. Schoenoprasum* and *A. ursinum* at meiosis (LEVAN, unpublished) furnish certain clues with

regard to the structural changes within an *Allium* idiogram, that is, partly as to the direction in which such changes may occur and partly as to the limits of the viability of new chromosome types. I shall briefly summarize some experiences of the origin of chromosome-morphologically new types of chromosomes by X ray treatment of diploid species of *Allium*.

By fragmentations medianly inserted chromosomes can become more or less terminally inserted. If large particles of a chromosome are lost so that only the portion in the neighbourhood of the pole spindle attachment is left then small independent chromosome fragments are formed. These terminally inserted chromosomes, as well as the diminutive chromosomes, look like corresponding chromosome types in untreated material. They can also pass through mitosis in a normal manner and thus possess a certain measure of viability.

If an attachment of the fragment to a chromosome is also added to a fragmentation there is present a translocation. Then either of the following two cases may happen:

1. The fragment lacks an insertion. The new type of chromosome should be at once viable. These translocated fragments have often been found to be attached to threads of varying lengths. In terminal translocations the new chromosome then resembles the s chromosomes of untreated material. Median translocations, common in X ray treated material, may also occur in untreated material.

2. The fragment has an insertion of its own. Chromosomes with 2 insertions arise. They are not at once viable unless the 2 insertions happen to be situated so close to each other that they act as a single insertion. Otherwise a break will take place sooner or later during an anaphase somewhere between the 2 insertions, which will of course result in the origin of new types of chromosomes (MATHER and STONE, 1933).

To sum up it may be said that X ray treatment has not been proved capable of altering the number of the pole spindle attachment, but it can bring about re-groupings in the chromatic substance associated with these attachments.

There is another fact, interesting from a chromosome-morphological point of view, to which attention should be called, with regard to species having both diploid and polyploid forms. In *A. nutans*, for instance, the diploid forms have only medianly inserted chromosomes. But in the autopolyploid series many different types of chromosomes

occur. Even the triploid forms of *A. nutans*, which I know of, have somatically 3 subterminally inserted chromosomes.

The hypothesis I put forward in a previous work (LEVAN, 1932) that the asymmetric chromosomes occurring within *Allium* are of a more derivative type, arisen through structural changes in more original, two-armed chromosomes, find some support in the facts mentioned above, thus:

1. The karyologically, in my opinion, most primitive species of *Allium*, those with 14 chromosomes, have almost exclusively medianly inserted chromosomes. The cytologically most derivative forms, those with 18 chromosomes, have proportionally more chromosomes with terminal insertion.

2. The origin of asymmetric chromosomes from symmetric has been observed direct during the X ray experiments.

3. In polyploid forms asymmetric chromosomes appear even if they are missing in corresponding diploid forms.

## II. CHROMOSOME SIZE AND CELL SIZE.

In order to find out whether there is any relation between the chromosome size and the cell size in the various species of *Allium*, large chromosomes necessitating large cells, I have made a number of measurements of the pollen length in the various species. If the results of such measurements are to be comparable it is necessary that all slides from which measurements are to be taken are prepared in exactly the same manner and that the pollen grains are in the same nuclear phase. These conditions I have tried to fulfil as closely as possibly. Further, allowance must be made for any great differences in the form of the pollen grains themselves. Thus, for instance, *A. scorodoprasum* has considerably more spherical pollen grains than the usual oval kind found in *Allium*. The pollen grain of this species has in this way relatively much too short a length.

The average measurements of 20 pollen grains of each species are given in the last column of Table 2. As appears from this Table there is no correlation at all between the chromosome size and the cell size. The *Allium* species, which has the largest pollen grains of all, *A. zebdanense*, has a chromosome size far below the average for all the species. Besides, the pollen length varies rather arbitrarily in proportion to the chromosome size. There is, however, a great variation in pollen length in the diploid species, from 22.5  $\mu$  to 44.3  $\mu$ .

This result agrees with DARLINGTON's case of size variation in the

chromosomes of *Tradescantia brevicaulis* (DARLINGTON, 1929). The flower bud, the chromosomes of which were 5 times smaller than normal, had nevertheless pollen of normal size. Chromosome size and cell size are evidently determined by different factors. There is a marked difference in effect when the chromosomes are increased in bulk and when they are increased in number. In the latter case a greater cell size is most frequently obtained.

### III. MEIOSIS.

The course of meiosis in *Allium* is that usually observed in chromatin-rich nuclei with long chromosomes. After zygotene pairing, which is generally complete, although sometimes disturbed by interlocking, there follows a long pachytene stage and then a diplotene stage with numerous loops. These loops rapidly decrease in number, partly because many of the chiasmata were not true ones and partly because 2 adjacent chiasmata frequently cancel out each other. Thus, the number of chiasmata falls from more than 20 to 4 or 5. At diakinesis the terminalisation is still slight, the estimated terminalisation coefficient being 0.1—0.2. At metaphase the terminalisation reaches its maximum, which varies very much in the different species, and quite surely also in different forms of the same species. In some instances the terminalisation coefficient was the following:

1. Terminalisation low (term. coeff. = 0.1—0.3):  
*A. narcissiflorum*, *A. albopilosum*, *A. ammophilum*.
2. Terminalisation moderate (term. coeff. = 0.5—0.6):  
*A. obliquum*, *A. Ostrowskianum*, *A. zebdanense*.
3. Terminalisation high (term. coeff. = 0.8—1.0):  
*A. flavum*.

The general rule in the bivalent form at metaphase I is that the 2-armed chromosomes with median constriction assume ring-form, while the subterminally or terminally inserted chromosomes form rods or asymmetric rings. The shorter the proximal chromosome arm is in the latter case the less frequently does the chromosome assume the form of a ring.

*A. zebdanense* furnishes a new instance of a direct proportionality between chromosome length and number of chiasmata in meiosis. This fact has in *Allium* been shown previously in *A. macranthum*, a species having 28 chromosomes (LEVAN, 1933 b).

The occurrence of a connection between the nucleolus and a pair

of chromosomes has been shown in the following species: *A. allopilosum*, *Ostrowskianum*, *Rosenbachianum*, *Schoenoprasum* and *zebdanense*. I have also found the same characteristic picture of the connection of the nucleolus with a pair of chromosomes in tetraploid species, for instance in *A. validum* ( $2n=28$ ). More suitable staining methods would certainly increase our knowledge of the behaviour of these *Allium* nucleoli. It might then be possible also to show the occurrence of the nucleolus in species in which it has not been detected with gentian violet staining.

In *Allium* there are species with localized chiasmata. As regards the earlier prophase stages I have not been able to discover any difference between species with localized chiasmata and species with random distribution. HUSKINS and SMITH (1934) have recently described the chromosome pairing in *Fritillaria Meleagris*, a species with localized chiasmata. They succeeded in showing that certain parts of the chromosomes are split already at leptotene and that just these split parts do not afterwards take part in the pairing. Even if the conditions observed in *A. Farreri* and *A. fistulosum* do not indicate a differential chromosome pairing, the assumption of such a pairing provides the most natural explanation of the origin of chiasma localisation in metaphase I. McCLINTOCK's observations (1933) of the pairing of non-homologous parts of chromosomes in *Zea mays* may supply an explanation why the chromosomes in *A. Farreri* and *A. fistulosum* appear to be paired along their entire length at pachytene. The evident random arrangement of the chiasmata in early diakinesis in the two *Allium* species is, however, difficult to explain. In many cases the chiasmata can be observed directly at this stage, and therefore the assumption of apparent chiasmata will not stand the test.

However, it is not probable that the localisation of the chiasmata is caused by any differences in the structure of the chromosomes but by genotypic control of the meiotic behaviour. The report of EMSWELLER and JONES (1934) of the heredity of the localisation of chiasmata is of interest in this connection. In a cross between *A. Cepa* and *A. fistulosum* they have observed that the localisation of chiasmata behaves like a recessive character. An observation that accords with this was made in *A. nutans* (LEVAN, unpublished). This species shows only random arrangement of the chiasmata. In an inbred progeny of a *nutans* form there occurred, however, one plant with localisation of chiasmata, evidently a recessive segregation. The localisation of

chiasmata is not confined to diploid species, it occurs, for instance, in *A. Porrum*, a 32-chromosome species.

The occurrence of an amphibivalent in *A. ammophilum* is the first case of segmental interchange within the *Liliaceae*. There is, it is true, a report published of ring-formation within *Brodiaea lactea* (SMITH, 1933), but in view of the high chromosome number of the species ( $n=21-24$ ) and the occurrence of species of *Brodiaea* with such a low chromosome number as  $n=5$ , one must in this case consider the possibility of multivalent formation. I have observed multivalent formation in other species of *Brodiaea*, and in *Allium* species with 42-48 chromosomes the occurrence of rings and chains of 4-6 chromosomes is very common.

*A. ammophilum* is a structural hybrid with the chromosomes  $ab\ cd\ ad\ cb$ . Such an interchange may arise, as DARLINGTON has suggested, as the result of crossing-over between two medianly homologous chromosome parts in two otherwise non-homologous chromosomes.

The pachytene stage in *A. ammophilum* shows that the pairing of the amphibivalent is completed later than the pairing of the usual bivalents. The cause of this should perhaps be sought in mechanical obstacles. The consequence of this is important, that is, the percentage of crossing-over in the amphibivalent must be reduced, indeed, a certain part of the middle of the chromosomes forming part of the amphibivalent is probably devoid of crossing-over.

### SUMMARY.

1. The chromosome morphology in mitosis and meiosis of some diploid *Allium* species is described.

2. One case of amphibivalent formation occurs in a diploid species, *A. ammophilum*.

3. *A. Farreri* offers a new example of chiasma localisation in meiosis.

4. In *A. zebdanense* a direct proportionality between chiasma number and chromosome length is shown.

5. The chromosome morphology of the *Allium* idiograms hitherto known is discussed, and the conclusion is drawn that the asymmetric chromosomes are derived from medianly constricted chromosomes by structural changes.

6. The chromosome size in different diploid species is demonstrated not to have any direct relation to the pollen grain size.

Hilleshög, Landskrona, December 1934.



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# GEUM URBANUM L. $\times$ G. RIVALE L.

## WEITERE UNTERSUCHUNGEN ÜBER EINE FORM, DEREN BLÄTTER DURCH KÄLTE WEISSBUNT WERDEN

VON D. ROSÉN

KLIPPAN, SCHWEDEN

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IN einer vor kurzem erschienenen Arbeit habe ich (ROSÉN 1933) über eine durch wiederholte Kreuzung (Kreuzung I und II) entstandene Form von *Geum urbanum*  $\times$  *rivale* mit im Frühjahr weissbunten Blättern berichtet. Dort habe ich hervorgehoben, dass diese Form kälteempfindlicher als die gewöhnlichen Formen dieses Bastards sein dürfte und dass die weissbunten Blätter durch den Einfluss der Kälte entstehen dürften. Hier soll berichtet werden über meine weiteren Studien über den Einfluss der Kälte auf die Entstehung der weissbunten Blätter dieser kälteempfindlichen Form sowie über einige Reinzüchtungs- und Kreuzungsexperimente, die ich ausgeführt habe um die Entstehung der weissbunten Form klarzulegen.

### KÄLTEUNTERSUCHUNGEN.

Bei meinen früheren Untersuchungen habe ich gefunden, dass weder ein Mangel an Licht oder Nahrungsstoffen die Ursache der Entstehung der weissbunten Blätter ist und dass von sonstigen Ursachen der Einfluss der Kälte die einzige mögliche zu sein scheint. Bei meinen weiteren Untersuchungen wollte ich natürlich in erster Linie hierfür Bestätigung erhalten. Hier soll über einige Experimente berichtet werden, die ich zu diesem Zwecke ausgeführt habe.

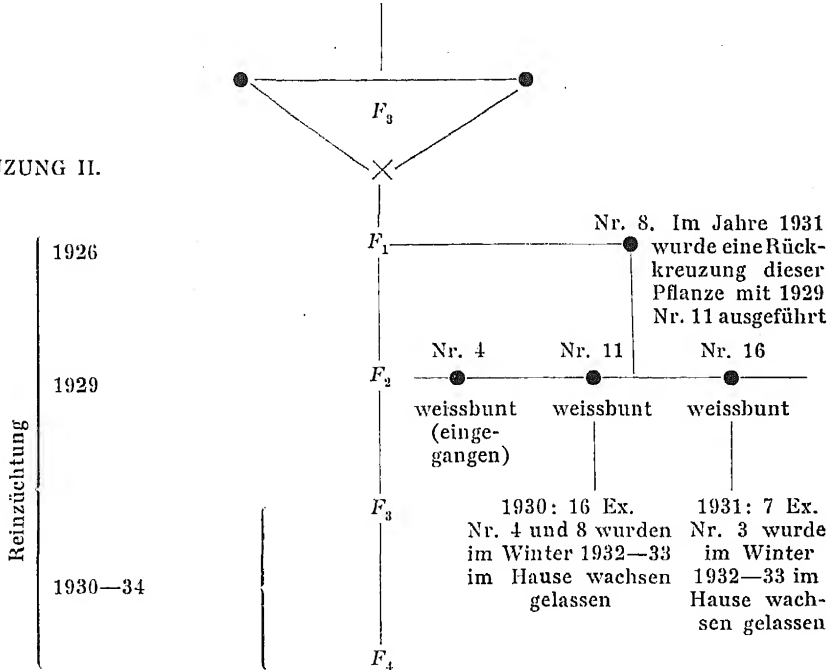
#### EXPERIMENT I.

Eine der weissbunten Stammpflanzen, 1929 Nr. 11, wurde im Sommer 1932 in zwei zerteilt. Die eine der so erhaltenen Pflanzen wurde wieder an der früheren Stelle im Freien ausgepflanzt. Die zweite wurde in einen Topf gesetzt und im Hause bis zum folgenden Sommer wachsen gelassen. Die Temperatur im Winter 1932—33 erreichte an der Stelle der ersteren — 15°. (Der Boden war da seit einiger Zeit von einer Schneeschicht bedeckt und die Temperatur wurde unter dem

Kurze Übersicht über Kreuzung I und II sowie Reinzüchtung der weissbunten Stammpflanzen.

KREUZUNG I. *Geum urbanum* L. ♀ × *G. rivale* L. ♂.

KREUZUNG II.



Schnee am Boden gemessen.) Im letzteren Falle betrug die niedrigste Temperatur  $+4^{\circ}$ . (Hier gleichwie im folgenden ist die Temperatur in Celsius $^{\circ}$  angegeben.) Im Frühjahr 1933 zeigte sich ein scharfer Unterschied im Aussehen der beiden Pflanzen. Die im Freien gepflanzte entwickelte gleichwie im vorherigen Jahr zuerst weissbunte und dann gelbgrüne Blätter. Die an gleicher Stelle kultivierten normal grünen Pflanzen entwickelten wie früher im Frühjahr und Vorsommer nur ganz grüne Blätter.

Die im Hause und bei niedrigst  $+4^{\circ}$  kultivierte Pflanze entwickelte keine weissbunten sondern nur gelbgrüne—hellgrüne Blätter, die bald eine ganz grüne Farbe annahmen. Die an gleicher Stelle kultivierten normal grünen Pflanzen entwickelten nur grüne Blätter.

Dieses Experiment scheint mir zusammen mit den früher angeestellten Versuchen und Beobachtungen vollkommen meine Ansicht zu bestätigen, dass die Weissbuntheit der Blätter erst durch den Einfluss der Kälte zu Tage tritt. Folgende Experimente bestätigen des weiteren diese Auffassung.

## EXPERIMENT II.

Durch im Jahre 1929 ausgeführter Reinzüchtung der weissbunten Stammpflanze 1929 Nr. 11 wurden nach Saat im Jahre 1930 16 Pflanzen erhalten, die im Herbst 1930 im Freien ausgepflanzt worden sind. Ein Teil dieser Pflanzen ist im Laufe der Jahre eingegangen. Die überlebenden haben nach Einwirkung der Winterkälte jedes Frühjahr *zuerst weissbunte* und dann gelbgrüne Blätter entwickelt. Zwei dieser Pflanzen, 1930 Nr. 4 und 8, wurden im Vorsommer 1932 in Töpfe gesetzt (Nr. 4 = Fig. 3, S. 84, ROSÉN 1933) und von Sommer 1932—Herbst 1933 im Hause kultiviert. Die niedrigste Temperatur hat hier  $+4^{\circ}$  betragen. Im Frühjahr 1933 entwickelten diese Pflanzen *keine weissbunten Blätter* sondern gelbgrüne—hellgrüne, die bald ganz grüne Farbe annahmen. Die an gleicher Stelle kultivierten normal grünen Pflanzen entwickelten, wie früher (Exp. I) erwähnt worden ist, nur grüne Blätter. Die übrigen weissbunten Pflanzen des Jahres 1930, die fortwährend im Freien kultiviert worden sind, entwickelten im Frühjahr 1933 wie früher *zuerst weissbunte*, dann gelbgrüne Blätter. Die an gleicher Stelle kultivierten normal grünen Pflanzen entwickelten *nur grüne Blätter*. *Dieses Experiment bestätigt demnach des weiteren die Auffassung, dass die Weissbuntheit der Blätter durch den Einfluss der Kälte an den Tag kommt.*

## EXPERIMENT III.

Um die Entstehung der weissen Blattpartien durch den Einfluss der Kälte festzustellen wurde noch ein Experiment angestellt. Hierzu wurde eine Pflanze benutzt, die von der weissbunten Stammpflanze 1929 Nr. 16 her stammt. Durch Reinzüchtung im Jahre 1930 wurden Samen erhalten, die nach Saat im Jahre 1931 7 Pflanzen gaben, die im Herbst 1931 im Freien ausgepflanzt worden sind. Während des Winters 1931—32 und des frühen Frühjahres 1932 sind 2 Pflanzen zugrunde gegangen. Die überlebenden 5 Pflanzen entwickelten im Frühjahr 1932 alle weissbunte Blätter. Eine dieser Pflanzen, 1931 Nr. 3 (= Fig. 2, S. 83, ROSÉN 1933), wurde im Vorsommer 1932 in einen Topf gesetzt und bis zum Sommer 1933 im Hause kultiviert. Die Minimumtemperatur betrug hier  $+4^{\circ}$ . Im Frühjahr 1933 entwickelte diese Pflanze zuerst 3 gelbgrüne Blätter mit *sehr kleinen weissen Partien* an den Rändern derselben, darauf gelbgrüne Blätter, die gar keine weissen Partien zeigten. Die kleinen weissen Blattpartien verblieben gleichwie bei den früher beschriebenen weissbunten Pflanzen unverändert. Die

gelbgrünen Blätter und Blattpartien nahmen dagegen allmählich grüne Farbe an.

Diese Pflanze zeigte also gegen Kälte eine grössere Empfindlichkeit als die weissbunten Pflanzen im Exp. I und II. Im Prinzip stimmt indessen Experiment III mit I und II überein. Als diese Pflanze im Winter 1932—33 im Hause bei *niedrigst*  $+4^{\circ}$  kultiviert worden ist, entwickelte sie im Frühjahr 1933 Blätter mit *sehr kleinen weissen Partien*. Als die gleiche Pflanze im Winter 1931—32 *starker Kälte ausgesetzt worden ist*, entwickelte sie im Frühjahr 1932 Blätter mit *grossen weissen Partien*. Durch stärkere Kälte wurde also die Grösse der weissen Partien in hohem Grade erhöht. Auch dieses Experiment bestätigt also die Auffassung, dass diese Pflanzen kälteempfindlicher sind als die übrigen Formen von *Geum urbanum*  $\times$  *rivale* und dass die weissbunten Blätter nach Kälteeinwirkung, bzw. Einwirkung von niedriger Temperatur entwickelt werden.

*Damit muss als festgestellt erachtet werden, dass das Auftreten von Weissbuntheit bei den Blättern dieser kälteempfindlichen Pflanzen auf den Einfluss der Kälte, bzw. den Einfluss der niedrigen Temperatur zurückzuführen ist.*

### VERERBUNGSUNTERSUCHUNGEN.

Mein grösstes Interesse in bezug auf die weissbunten Pflanzen richtete sich auf die Klarlegung ihrer Entstehung und auf das Studium einiger damit zusammenhängenden Probleme. In dieser Hinsicht habe ich einige Reinzüchtungs- und Kreuzungsexperimente angestellt. Diese Experimente sind unter allen denkbaren Vorsichtsmassnahmen zur Ausführung gelangt. Die Isolation der Blüten ist stets mit Pergamenttüten geschehen.

Später hoffe ich ausführlicher über die ausgeführten Reinzüchtungs- und Kreuzungsexperimente berichten zu können. Hier sollen nur zwei derselben kurz berührt werden.

#### REINZÜCHTUNG DER PFLANZE 1926 NR. 8.

Durch Reinzüchtung dieser Pflanze wurden erhalten:

	Anzahl normal grüne Pflanzen	weissbunte Pflanzen
1929 .....	95	3
1933 .....	12	1
1934 .....	336	27
	443	31

In sämtlichen Fällen ist also eine deutliche Spaltung erhalten worden. Eine Beurteilung der Spaltungszahlen will ich indessen erst vornehmen, wenn einige komplettierende Untersuchungen abgeschlossen sind.

Am einfachsten dürfte die weissbunte Form als eine rezessive Form aufzufassen sein.

Bei Reinzüchtung der weissbunten Pflanzen sind nur Individuen erhalten worden, die *nach Kälteeinwirkung* weissbunte Blätter entwickelt haben. *Irgendwelche reinweissen Formen* habe ich bei den Keimungsexperimenten nicht beobachten können. Auch sind keine Pflanzen erhalten worden, die *nach Kälteeinwirkung* — Überwinterung im Freien — *rein grüne Blätter* entwickelt haben.

Beim ersten Überwintern im Hause, im Winter 1929—30 (ROSEN 1933, S. 83), entwickelte die überlebende Pflanze keine weissbunten Blätter. Auf Grund des geringen Materials, das in genannter Arbeit zur Beurteilung vorlag, wagte ich es nicht eine Ansicht über diese Erscheinung zu äussern. Nunmehr dünkt es mir wahrscheinlich, dass diese Pflanze, die bald eingegangen ist, und also nie der Einwirkung von Kälte ausgesetzt worden ist, nicht normal grün gewesen ist.

Würden die weissbunten in weissbunte und normal grüne aufspalten, so sollten die letzteren als mehr vital ausgebildet worden sein und in einer der Generationen der späteren Jahre fortgelebt haben. Da dies nicht der Fall ist, scheint mir alle Wahrscheinlichkeit dafür zu sprechen, dass die oben genannte Pflanze nicht normal grün sondern weissbunt gewesen ist und dass sie in Übereinstimmung mit den weissbunten Pflanzen im Experiment I und II nach Überwinterung im Hause keine weissbunten Blätter entwickelt hat.

#### KREUZUNGSEXPERIMENTE.

Um die Entstehung der weissbunten Form klarzulegen habe ich einige Kreuzungsexperimente ausgeführt. Hier soll über eines dieser berichtet werden, eine Rückkreuzung einer der weissbunten Stammpflanzen mit der Mutterpflanze. Nach Kreuzung im Jahre 1931 der Pflanze 1926 Nr. 8 ♀ mit 1929 Nr. 11 ♂ wurden Samen erhalten, die nach Saat im Jahre 1932 41 Pflanzen gaben. Diese wurden im Herbst 1932 im Freien ausgepflanzt. Während des Winters 1932—33 und des frühen Frühjahres 1933 sind 15 Pflanzen eingegangen. Von den im Mai 1933 überlebenden zeigten 23 normal grüne Blätter, während 3 weissbunte Blätter haben. Auch hier hatte also eine Spaltung stattgefunden. Die Anzahl der eingegangenen Individuen ist indessen so

gross, dass sichrere Schlussätze in bezug auf die Art der Spaltung erst nach komplettierenden Untersuchungen gezogen werden können.

Durch das ausgeführte Kreuzungsexperiment und durch die Reinzüchtungsexperimente ist in einer Hinsicht volle Klarheit erhalten worden. Durch die ausgeführten Experimente ist offenbar gezeigt worden, dass die Mutterpflanze der weissbunten Pflanzen, 1926 Nr. 8, heterozygoter Natur hat. Damit ist also die Frage nach der Entstehung der weissbunten Form (ROSÉN 1933, S. 89) teilweise klargelegt. Diese Form entsteht durch Ausspaltung unter den Nachkommen der heterozygoten Mutterpflanze, 1926 Nr. 8. Es verbleibt nun die weitere Frage wie diese heterozygote Form entstanden ist. Um in dieser Hinsicht womöglich Klarheit zu gewinnen sind Experimente bereits im Gange.

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Nachdem die Entstehung und die Vererbungsverhältnisse der weissbunten Form durch weitere Untersuchungen näher klargelegt worden sind, will ich einen Vergleich mit den experimentellen Resultaten früherer Studien auf diesem Gebiete anstellen. Es sollen hier nur einige bemerkenswertere Fälle von Weissbuntheit durch Kälteeinwirkung in Kürze angeführt werden.

Weissbuntheit ist eine in der Pflanzenwelt sehr häufige Erscheinung. Ich will hier nur auf die angeführten zahlreichen Fälle in einer Reihe von Arbeiten hinweisen, z. B. CORRENS (1919—31), SCHÜRHOFF (1924), KÜSTER (1925, 1926, 1927), SCHWARZ (1928) u. a.

*Weissbuntheit infolge Einflusses von Kälte bzw. niedriger Temperatur* ist dagegen eine seltenere Erscheinung. Ich will hier einige bemerkenswertere Fälle anführen. MOLISCH (1901) hat durch Experimente nachgewiesen, dass bei einer Form von *Brassica oleracea acephala* Weissbuntheit bei einer Temperatur von  $+4$  bis  $+7^{\circ}$  auftritt. KANGIESSER (1913) hat durch Kälte verursachte Weissbuntheit bei *Oxalis acetosella* L., KIESSLING (1918) bei *Lamium maculatum* L. nachgewiesen. FIGDOR (1914) hat das Auftreten von Weissbuntheit bei *Funkia lancifolia* SPRING bei einer Temperatur von  $+9$  bis  $+13^{\circ}$  nachgewiesen.

Bei den Getreidearten sind mehrere Fälle nachgewiesen. So hat GASSNER (1915) Experimente mit einer Hafersorte von La Plata ausgeführt, die bei niedriger Temperatur,  $+1$  bis  $+2^{\circ}$  C, weissbunte Blätter entwickelt. COLLINS (1927) hat eine Gerstenform gefunden, die bei niedriger Temperatur weissgestreifte Blätter ausbildet. Beim

Roggen ist durch Kälteeinfluss verursachte Weissbuntheit von BUCHINGER (1932) nachgewiesen worden.

Einige weitere Fälle sind nachgewiesen worden. So hat SCHWARZ (1930) Experimente mit einer Form von *Selaginella Marlesii* SPRING ausgeführt, die im Treibhaus normal grüne Blätter ausbildet, bei  $+10^{\circ}\text{C}$  und darunter aber weissgrüne Blätter. Von grossem Interesse scheinen mir FISCHBACHS (1933) Untersuchungen über *Linum hirsutum*  $\times$  *viscosum* und NOACKS (1934) über *Hypericum*-Bastarden zu sein.

Kurz vor der Veröffentlichung meiner früheren Arbeit erschien eine neue, ausführliche Arbeit über *Geum urbanum*  $\times$  *rivale* von PRYWER (1932). Auch in dieser Arbeit wird indessen beim Bericht über die  $F_2$ -Generation nichts über eine weissbunte Form erwähnt.

### ZUSAMMENFASSUNG.

1. Durch die ausgeführten Kälteexperimente ist festgestellt worden, dass die Weissbuntheit der Blätter der in Frage stehenden Form von *Geum urbanum*  $\times$  *rivale* nach Einwirkung von Kälte, bzw. niedriger Temperatur auftritt.

2. Durch weitere Reinzüchtungs- und Kreuzungsexperimente ist klargelegt worden, dass die weissbunte Form durch Ausspaltung unter den Nachkommen einer heterozygoten grünen Mutterpflanze aufgetreten ist.

3. Durch weitere Experimente werde ich versuchen Klarheit in bezug auf die Entstehung dieser sowie hinsichtlich damit im Zusammenhang stehender Probleme zu erhalten.

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# DIE ANALYSE DER SYNTHETISCH HERGESTELLTEN *SALIX LAURINA*

VON HERIBERT NILSSON

LUND

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IN mehreren Abhandlungen habe ich früher über das Entstehen der Gartenart *Salix laurina* (SM.) WILLD. aus der  $F_2$  des Bastards *S. viminalis* L.  $\times$  *caprea* L. berichtet (HERIBERT NILSSON 1918, 1928, 1930). Diese extravagante Kombination wurde anfangs als ganz steril betrachtet, da nach freiem Abblühen kein einziger Samen erhalten wurde, und weil meine ersten Kreuzungsversuche auch alle ganz versagten.

Während der Jahre 1929 und 1930 wurden indessen Kreuzungen in grossem Maassstabe mit dem synthetischen Strauch, *S. laurina* f. *artefacta*, ausgeführt. Dieser Strauch ist, wie der Gartenklon, *S. laurina* f. *hortensis*, weiblich. Als ♂-Eltern wurden die Arten *S. caprea*, *cinerea*, *viminalis*  $\times$  *caprea*, ein triploider *gigantea*-Typus dieser Kreuzung, *nigricans* und *phylicifolia* verwendet. Die Kreuzungen mit den erstgenannten Arten und Bastarden ergaben erst auf mehrere Tausend von Samenanlagen einen Samen. Entschieden besser war das Resultat der *nigricans*- und *phylicifolia*-Kreuzungen. *S. laurina* erinnert auch, wie früher auseinandergesetzt, sowohl in bezug auf die Blattmorphologie als bezüglich der Chromosomenzahl an diese Arten. HÅKANSSON (1929) hat in der Meiosis zirka 40 Chromosomen gefunden. Da man früher glaubte, dass *S. phylicifolia* 44 n-Chromosomen hat (BLACKBURN and HARRISON 1924, HÅKANSSON 1929), *S. cinerea* 38, schien ja die Übereinstimmung mit diesen Arten ziemlich gut. Der junge Schüler WINGES, SKOVSTED (1929), hat — wohl mit dem Munde des Lehrers — ausgesprochen, dass die zytologischen Verhältnisse darauf hinweisen, dass *S. laurina* ein Bastard zwischen *S. cinerea* ( $n=38$ )  $\times$  *phylicifolia* ( $n=44$ ) sei, was man auch früher auf Grund von floristischen Beobachtungen vermutet hatte. Das ist ja sehr gut. Da ich indessen *S. laurina* unter ganz sicheren Kautelen experimentell hergestellt hatte, war ja meine Auffassung ebenso sicher wie als Annahme wenig kühn. Es zeigte sich auch bald, dass die Prämissen der SKOVSTEDSchen Verneinung des Experiments, wie ja kaum anders zu erwarten war, falsch waren.

Die Bestimmung der Chromosomenzahl von *S. phyllicifolia* L. (*S. Weigelliana* WILLD.) schien mir sehr zweifelhaft. Denn für *S. Andersoniana* SM. (*S. nigricans* (SM.) FR.) hatten BLACKBURN und HARRISON die hexaploide Zahl ( $n=57$ ) gefunden. Da Kreuzungen zwischen diesen Arten sehr leicht gelingen, da die  $F_1$ -Sträucher ganz fertil sind, und da die Arten über den grössten Teil des mittleren und nördlichen Schwedens eine gemischte Population bilden, war kaum zu erwarten, dass sie eine abweichende Chromosomenzahl haben sollten. Eine erneute Untersuchung von *S. phyllicifolia* durch HÅKANSSON (1933, p. 201 u. f.) ergab auch die haploide Zahl 57, also ganz mit *S. nigricans* übereinstimmend. Damit ist auch die kühne Annahme SKOVSTEDS, dem Experimente widersprechend und ohne jede salikologische Erfahrung, seine ganz unsinnige Verneinung einer Tatsache, auch zytologisch ungereimt, weil die Prämissen falsch sind.

Da es wirklich so anspruchsvolle Personen gibt, dass sie nicht einmal an die experimentelle Synthese glauben können, entschloss ich mich, durch die oben erwähnten Kreuzungsversuche in grossem Massstabe eine *Analyse* der *S. laurina* durchzuführen, in der Hoffnung, diesen extravagantesten und an die Arten der Gruppe *Virescentes* (*nigricans*, *phyllicifolia*) mehr als an ihre Eltern (*caprea*, *viminialis*) erinnernden Typus in ihre wahren Stammarten zu zerlegen. Wäre der *laurina*-Typus noch ziemlich heterozygot, so könnte man schon in  $F_1$  der Kreuzung ein Resultat erwarten. Es galt nur noch eine Art zu finden, die einen guten Analysator bildete. Die beste Art war in dieser Hinsicht nicht *S. cinerea*, wie man auf Grund der vermuteten Chromosomenzahl erwarten sollte, sondern *S. phyllicifolia*, die *S. laurina* in gewissen Merkmalen ähnelte. Nach Kreuzung von *S. laurina*  $\times$  *cinerea* erhielt ich nur sehr wenige Samen, die 6 Sträucher lieferten. Nur ein Individuum war mittelkräftig, die übrigen schwach, einige chlorotisch, bald absterbend. Diese Art war also als Analysator ungeeignet.

Nach Kreuzung von *S. laurina*  $\times$  *phyllicifolia* erhielt ich zwar spärlichen Samenansatz, jedoch auf einige Hundert Ansatzmöglichkeiten einen Samen. Sie waren von verschieden guter Entwicklung und Keimungsfähigkeit. Als Resultat wurden alles in allem 29 Sträucher erhalten. Die Nachkommenschaft ist zwar klein, da sie aber sowohl die mit der Kreuzung zu lösende Frage beantwortet als auch neue Probleme aufgeworfen hat, habe ich über das Resultat schon jetzt berichten wollen.

Die Mehrzahl der Nachkommen war zwischen *S. laurina* und *S. phyllicifolia* intermediär. Der erstgenannte Typus ist ja ziemlich

breitblättrig (HERIBERT NILSSON 1928, Taf. VI u. VII), mit der grössten Breite gleich oberhalb der Mitte. Die Blätter der *S. phylicifolia* ♂ waren schmal umgekehrt eiförmig. Die Blätter der Nachkommen schwankten zwischen schmaler und breiter umgekehrt eiförmig. Die Länge betrug, wie bei den Eltern, das 2—3-fache der Breite. Die Kahlheit der Zweige und Blätter der *S. phylicifolia* dominierte, was ich auch früher in Kreuzungen mit dieser Art gefunden habe. In bezug auf Kräftigkeit, Gestaltung, Farbe und Glanz der Blätter, Blütenreichtum, Ähren- und Kapselform war die Variabilität gross. Von den Sträuchern war nur ein einziger männlich, die übrigen 28 weiblich. Ein Individuum war schwach intersexuell. Der ♂-Strauch war pollenreich, und mehr als die Hälfte des Pollens war dem Aussehen nach gut ausgebildet. Die weiblichen Sträucher waren, nur mit einer einzigen Ausnahme, ganz oder sehr stark steril.

Von den erwähnten Durchschnittsindividuen, die in einer ziemlich kontinuierlichen Reihe die Merkmale der Eltern kombinierten, was ja schon für eine starke Heterozygotie der *S. laurina* spricht, wich ein Individuum in sehr auffälliger Weise ab. Der Strauch war eine ebenso extreme Extravagante wie es *S. laurina* in ihrer  $F_2$ -Generation war. Da er eine noch ausgeprägtere Habitusänderung als *S. laurina* bezeichnete, aber in derselben Variationsrichtung, ferner vegetativ kräftig und grossblättrig war sowie ganz erstaunlich grosse Ähren hatte, habe ich diesen Typus *S. superlaurina* genannt.

Die langen, ganz schwarzbraunen und kahlen Zweige des Strauches verursachten mit den tiefgrünen, weissgeaderten, schimmernd glänzenden Blättern und mit den riesengrossen, trüb filzig graubehaarten Ähren bei der Frühlingsblüte ein ganz sonderbares Farbenspiel. Die Blätter waren beim Ausschlagen der Ähren sehr schwach entwickelt, sodass die Blüte fast vorläufig war, die Entwicklung der Blätter schritt aber dann sehr schnell fort, sodass die Jahreszweige bei voller Blüte schon halb-grosse Blätter trugen. In dieser Hinsicht näherte sich der Strauch den Grosseltern, *S. caprea* und *viminalis*.

Die Blätter waren im ausgewachsenen Zustande fast *caprea*-gross und auch in bezug auf ihre Form sehr *caprea*-ähnlich (Fig. 1). Die grösste Breite hatten sie an der Mitte. Die *caprea*-Merkmale waren also in bezug auf den Blatttypus auffallend und viel ausgeprägter als bei *S. laurina*. Bei der Gonenbildung der *S. laurina* hat offenbar eine Abspaltung von *caprea*-ähnlichen Gameten stattgefunden. Bei der Kreuzung mit *S. phylicifolia* sind aber die *caprea*-Eigenschaften mit denen dieser Art kombiniert worden, weshalb ein Produkt zu erwarten ist,

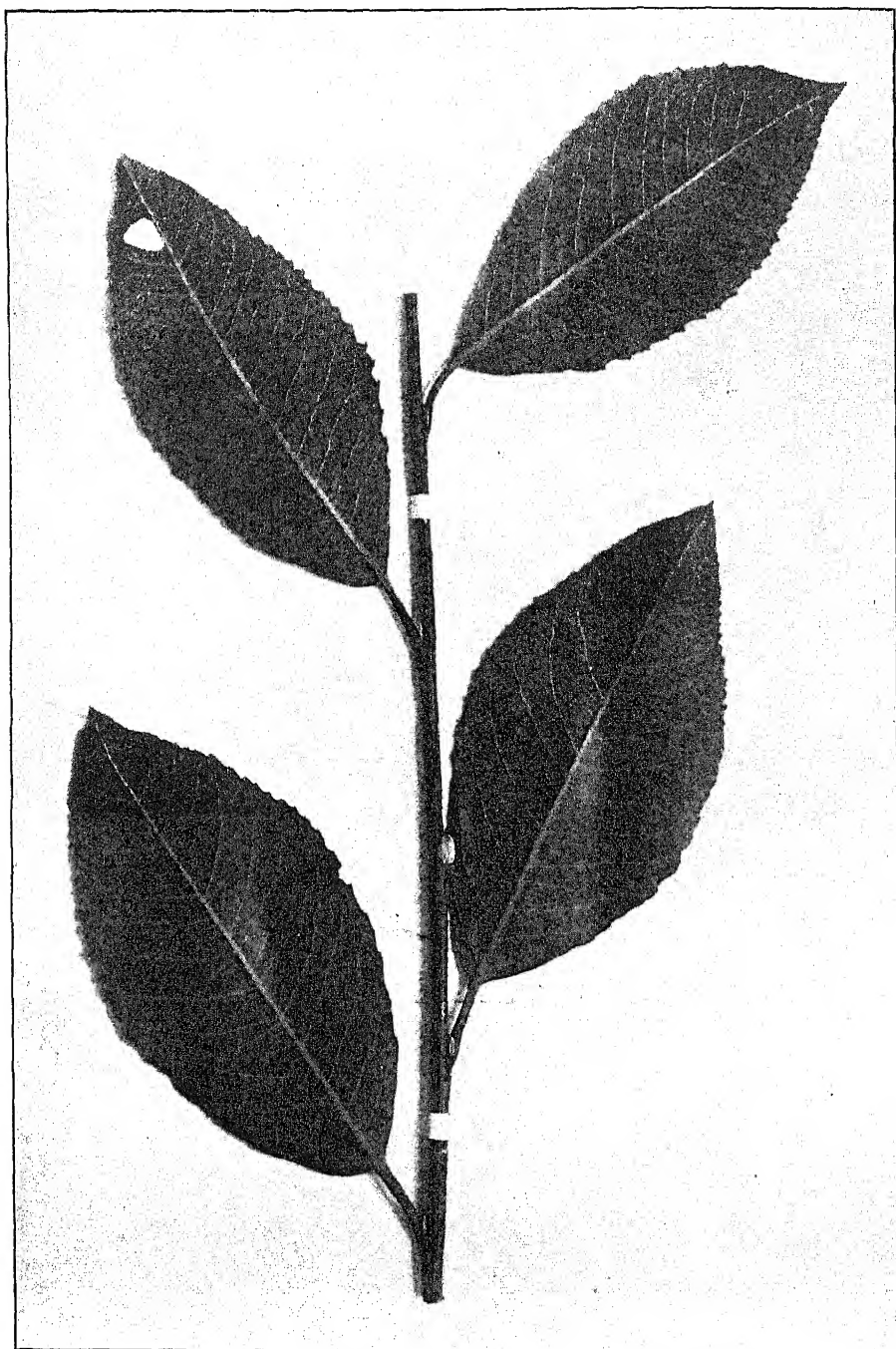


Fig. 1. *S. superlaurina*, mit Blättern von der Form und Grösse der *S. caprea*.



Fig. 2. Geschwisterindividuum der *S. superlaurina*, das Blätter von dem Aussehen eines Bastards *viminalis*  $\times$  *phylicifolia* hat.

das in gewisser Hinsicht einem Bastard *S. caprea*  $\times$  *phylicifolia* ähnlich erscheinen wird. Das ist auch wirklich der Fall in bezug auf die Blattcharaktere der *S. superlaurina*. Denn mit den oben erwähnten *caprea*-Merkmalen vereinigen sie die Farbe und den Glanz, weiter die roten Blattstiele und Mittelnerven der Blattunterseite sowie auch die starke Kahlheit der *phylicifolia*-Blätter. Die jungen Blätter sind ganz kahl, die ausgewachsenen Vorsommerblätter schwach *laurina*-behaart (oberseitig, und unterseitig fast nur gegen den Mittelnerv), die Spätsommerblätter sind wieder ganz kahl. Falls man also auf die Bastardherkunft des Strauches auf Grund des Blatttypus schliessen wollte, wäre die Annahme einer Hybride *S. caprea*  $\times$  *phylicifolia* die weitaus wahrscheinlichste. Dieser Bastard ist aber im Experimente nicht realisierbar, was ich mehrmals habe konstatieren können.

Ausser den Merkmalen der erwähnten Arten traten indessen Blattcharaktere auf, die ganz befremdend wirkten. Die Blätter wurden sehr derb, die Aderung als weisses Muster oberseitig scharf hervortretend, die Ränder scharf und unregelmässig, etwas ausgebissen gesägt; unterseitig waren die jungen Blätter des Jahreszweiges deutlich glaucescent, die ausgewachsenen dagegen matt grün oder weissgrün. Diese Merkmale sind bei keinem der Eltern zu finden, sie erinnern eher an eine so fernstehende Art wie *S. myrsinites*.

Nicht minder auffallend waren die Ähren. Schon die riesengrossen, grauen Ähren zusammen mit den halbentwickelten, glänzend grünen Blättern machten einen befremdenden Eindruck. Am meisten stimmte der Typus der Ähren und der Kapseln mit *S. laurina* überein, die indessen in dieser Hinsicht sehr extravagant ist. Nur waren alle Masse bedeutend grösser, fast verdoppelt. In bezug auf die Grösse der Ähren übertrifft *S. superlaurina* sämtliche schwedischen *Salix*-Arten, was auch aus Fig. 3, die natürliche Grösse zeigt, sehr gut hervorgeht. Von anderen *Salix*-Arten scheint nur die ganz sonderbare und von allen anderen Arten weit abweichende chinesische *S. magnifica* HEMS. grössere Ähren zu haben. Sie sind aber sehr licht, fast *Populus*-ähnlich.

Die Blätter der Ährenstiele waren klein, ganzrandig. Die Kapseln waren flaschenförmig mit langem Hals, deutlich gestielt (der Stiel jedoch kaum  $\frac{1}{4}$  der Kapsellänge betragend), grob filzig behaart mit durchschimmerndem Grün der Oberfläche, sodass sie grünlich bis fast gelblich silberweiss aussahen. Der Griffel war deutlich verlängert, bis 2 mm lang, die Narben kürzer, fast regelmässig gespalten.

*S. superlaurina* ist also offenbar ein mehr *caprea*-ähnliches Spal-

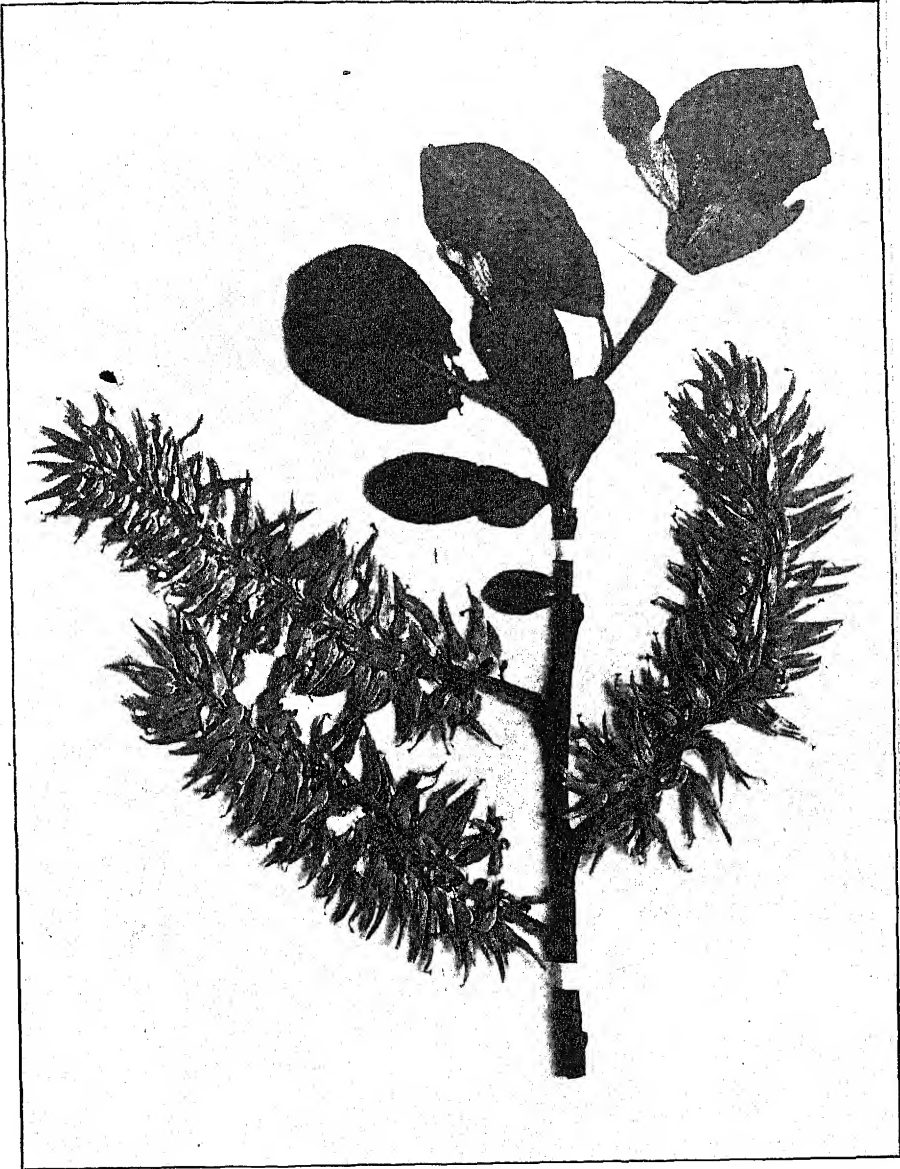


Fig. 3. Riesenähren der *S. superlaurina*.

tungsprodukt als *S. laurina*. Dass indessen diese nicht nur in bezug auf die *caprea*-Eigenschaften heterozygot ist, was vielleicht zu erwarten wäre, da sie morphologisch capreoklin ist, sondern auch *viminalis*-Gene führt und auch in bezug auf diese heterozygot ist, zeigt weiter die



Nachkommenschaft. Diese war im allgemeinen zwischen den Eltern, *S. laurina* und der mehr schmalblättrigen *S. phylicifolia*, intermediär, aber bei einem Strauch waren die Blätter bedeutend schmaler und länger (Fig. 2). Er ähnelte in dieser Hinsicht dem von mir experimentell hergestellten Bastard *S. viminalis*  $\times$  *phylicifolia* (HERIBERT NILSSON 1930, Taf. XV) und ebenso meiner ebenfalls artifiziiell produzierten Verbindung *S. (viminalis*  $\times$  *caprea*)  $\times$  *phylicifolia*.

Werden nun die beiden Extreme der Variabilität der Verbindung *S. laurina*  $\times$  *phylicifolia*, nämlich Fig. 1 und 2, verglichen, so erhält man einen frappanten Ausdruck für die Spaltung der *S. laurina*. Diese muss offenbar eine Gamete gebildet haben, die das Genom des einen Elters, *S. caprea*, annähernd restituiert hat, denn bei Kreuzung mit *S. phylicifolia* wird ein Strauch erhalten, der stark den Eindruck eines Bastards *S. caprea*  $\times$  *phylicifolia* macht. *S. laurina* muss indessen weiter auch eine Gamete gebildet haben, deren Genom dem des anderen Elters, *S. viminalis*, ähnlich gewesen ist, denn es wird ein Strauch erhalten, der *S. viminalis*  $\times$  *phylicifolia* nahe kommt. *S. laurina* bildet also, obgleich morphologisch sehr extravagant, Gameten, die denen ihrer Eltern ähnlich sind. Ich habe also *S. laurina* nicht nur synthetisch aus *S. viminalis*  $\times$  *caprea* experimentell dargestellt, sondern sie nun auch in ihre Elternkomponenten analytisch aufgelöst. Ich wage also zu sagen, dass die wahre Natur keines aberranten Spaltungsprodukts so streng bewiesen ist wie die der *S. laurina*.

Wie ist nun *S. laurina* aus ihren unwahrscheinlichen Eltern konstituiert worden? Weshalb macht sie in gewissen Merkmalen den Eindruck einer *phylicifolia*-Kreuzung? Ja, das sind Fragen, die vom Ausgangspunkt ihrer festgestellten Abstammung diskutiert werden können, kaum aber fruchtbar mit einer fortwährend frei angenommenen. An Skovstedianismus hat es bei *S. laurina* nicht gefehlt, da man früher nicht weniger als 12 verschiedene Eltern angenommen hat (HERIBERT NILSSON 1928, p. 52).

Durch die Untersuchung von HÅKANSSON (1929) ist gezeigt worden, dass der Typus hypertetraploid ist. Die exakte Chromosomenzahl hat er aber wegen Unregelmässigkeiten in der Meiosis nicht feststellen können. Er vermutet 41—42. Eigentümlich erscheint, dass bei der grossen Sterilität des Strauches die Bivalentenbildung sehr gut ist. Dies spricht ja für eine genetische Verwandtschaft der Chromosomen, wie sie auch von HÅKANSSON (1929) für die  $F_1$  und  $F_2$  der Kreuzung *S. viminalis*  $\times$  *caprea* nachgewiesen worden ist.

Es scheint mir, als ob sowohl die Hypertetraploidie wie die fast

vollständige Chromosomenbindung in einer sehr einfachen Weise erklärt werden könnte. HÅKANSSON hat gezeigt, dass bei der Teilung der PMZ Dyaden mit der diploiden Chromosomenzahl gebildet werden (1929, p. 8). Auch bei einem so fertilen Bastard findet also diese, bei stark sterilen Bastarden nicht ungewöhnliche Erscheinung, statt. Dass diese Gameten auch funktionsfähig sind, wird dadurch gezeigt, dass ich bei *S. caprea* × *viminalis* unter den bis jetzt aufgezogenen 636 Pflanzen mindestens 6, vielleicht eher 10 Triploiden gefunden habe, was jedenfalls mindestens 1 % diploide Gameten anzeigt. Es erscheint mir daher kaum gewagt, weiter anzunehmen, dass tetraploide Gameten gebildet werden können, wie dies auch z. B. in den Versuchen über *Raphanobrassica* von KARPECHENKO (1927) gefunden worden ist. Falls eine tetraploide Gamete in  $F_1$  gebildet wird, und falls diese mit einer normalen haploiden, was ja das wahrscheinlichste ist, konjugiert, muss natürlich in  $F_2$  eine hypertetraploide Pflanze gebildet werden; aber in diesem Falle keine Aneuploide, sondern eine Pentaploide. *S. laurina* wäre also, falls diese Annahme richtig ist, eine pentaploide Aberrante mit doppelten sowohl *caprea*- als *viminalis*-Genomen und ausserdem mit einem extra Rekombinationsgenom der Arten. Die starke Konjugation der Chromosomen wäre dann mit Hinsicht auf die doppelten Artgenome selbstverständlich, die Sterilität aber durch das teilungsstörende fünfte Genom auch erklärt. Weiter wäre die *phylicifolia*-Ähnlichkeit als ein Ausdruck für die Annäherung an die Chromosomenzahl dieser Art zu deuten.

Natürlich kann nur eine Untersuchung der somatischen Zahl der Chromosomen, was ja durch ihre Höhe erschwert ist, hierin völlige Klarheit bringen. Denn durch Tri- und Tetravalentbildung wird in der Meiosis die Zahl erniedrigt, durch Univalentbildung erhöht, und HÅKANSSON (1929) hat sämtliche Erscheinungen konstatiert. Falls man seine für eine Auszählung deutlichsten Bilder durchmustert, nämlich die der heterotypischen Metaphase (l. c. p. 29), findet man folgende Zahlen: 46, 44 und 55, durchschnittlich also 48,33. Aber 48 ist ja gerade die erwartete Zahl der Diakinese einer pentaploiden Pflanze mit vollständiger Paarung, nämlich  $\frac{95}{2} = 47$  Bivalente und 1 Univalent. Die Andeutung der pentaploiden Natur von *S. laurina* ist deshalb jedenfalls sehr stark.

Wenn nun *S. laurina* eine pentaploide Form ist, so erscheint es kaum eigentümlich, dass eine Kreuzung mit der hexaploiden *S. phylicifolia* besser gelingt als mit den diploiden Eltern. Dies war auch der

Fall. Aus der mehrmals und mit Tausenden von Blüten ausgeführten Kreuzung *S. laurina*  $\times$  *viminalis* habe ich keinen einzigen Samen erhalten. Die Verbindung *S. laurina*  $\times$  *caprea* hat einige wenige, obgleich durchweg verkümmerte Samen geliefert. Aus einem ziemlich wohlentwickelten Samen habe ich indessen einen Strauch aufgezogen, der eine normale, obgleich sehr langsame Entwicklung zeigte. Das doch ein wenig bessere Resultat der letzterwähnten Kreuzung ist um so eigentümlicher als mir die Kreuzung *S. caprea*  $\times$  *phylicifolia* niemals, die Verbindung *S. viminalis*  $\times$  *phylicifolia* recht gut gelungen ist.

In der Kreuzung *S. laurina*  $\times$  *phylicifolia* war der Samenansatz, wie oben erwähnt, zwar spärlich, aber es konnte doch eine Nachkommenschaft aufgezogen werden. Es war indessen zu erwarten, dass die Verbindung Pentaploide  $\times$  Hexaploide weitgehende Störungen in der Meiosis und grosse Sterilität der Nachkommenschaft verursachen wird. Dies traf auch ein. Nur der ♂-Strauch der Kreuzung und der *superlaurina*-Typus wichen hiervon ab, indem der erstere ziemlich guten Pollen ausbildete, der letztere vollkommene Fertilität zeigte, genau so gute wie die Elternarten *S. caprea*, *viminalis* und *phylicifolia*. Wie ist dies zu erklären?

Die grosse Vitalität und die riesigen Blätter und vor allem Ähren des *superlaurina*-Strauches erweckten den Verdacht, dass er ganz wie die triploiden *gigantea*-Formen eine Genomvermehrung darstellen könnte. Material des Strauches wurde deshalb HÅKANSSON für eine zytologische Analyse überlassen. Seine Untersuchung ist noch nicht abgeschlossen; so viel ist aber schon nach seiner mündlichen Mitteilung sicher, dass die  $2n$ -Zahl jedenfalls um 140—150 liegt. *S. superlaurina* ist also wahrscheinlich eine oktoploide Form. Diese Chromosomenzahl ist bei *Salix* selten, kommt aber nach den Untersuchungen des schwedischen Salikologen MARKLUND (HOLMBERG 1931, pp. 33 und 37) bei *S. myrsinites* und *S. glauca* vor, also bei hochnordischen Arten. Mit diesen Arten hat *S. superlaurina* gar keine Verwandtschaft. Sie gehört aber in bezug auf die extrem hohe Chromosomenzahl in ihre Klasse.

Da *S. phylicifolia* Gonen mit der Chromosomenzahl 57 ( $3 \times 19$ ) und *S. laurina* in ihren Gonen höchstens um 50 Chromosomen haben kann, dürften wohl gewöhnlich Nachkommen mit etwas mehr als 100 Chromosomen gebildet werden, also hypohexaploide oder vielleicht durch Elimination pentaploide Pflanzen wie die Mutterart. Die Geschwister der *S. superlaurina* repräsentieren wohl diese Zahlen. Aber der *superlaurina*-Typus hat ja eine Zahl, die auffallend grösser ist.

Es scheint mir deshalb, als ob dieser Typus nur durch die Annahme erklärbar wäre, dass er durch eine diploide *phylicifolia*-Gamete gebildet worden ist. Diploide Gonen hat HÅKANSSON (1933) tatsächlich für den ebenso wie *S. phylicifolia* hexaploiden Bastard *S. nigricans*  $\times$  *phylicifolia* konstatiert (l. c. p. 208). Durch eine diploide Gamete der *S. phylicifolia* und eine vielleicht durch Chromosomenelimination restituierte tetraploide Gamete der *S. laurina* könnte eine oktoploide Pflanze konstituiert werden. Denn die diploide Gamete der ersten Art ist ja eigentlich hexaploid ( $2 \times 3 \times 19$ ). *S. superlaurina* sollte also eine ternäre allopoloide Artverbindung darstellen die ausser dem Rekombinationsgenom von *caprea* und *viminialis* ein vollständiges *phylicifolia*-Genom enthält. Voraussetzung für diese Annahme ist indessen auch, dass die Genome der *S. caprea* und *S. viminialis* einerseits, der *S. phylicifolia* andererseits, nicht all zu stark inkompatibel sind. Meine weiteren Versuche ergänzen auch in dieser Hinsicht die Beweiskette.

Es wurde nämlich auch eine Bastardverbindung (*S. phylicifolia*  $\times$  *nigricans*)  $\times$  (*viminialis*  $\times$  *caprea*) herzustellen versucht. Sie ist gelungen, aber nur in bezug auf ganz vereinzelte Gametenkombinationen. Aus zirka 2250 gekreuzten Blüten und 9000 Samenmöglichkeiten resultierten nur 8 Samen. Diese waren aber sehr kräftig, ergaben 6 Pflanzen, die sich nun zu 5—6 m hohen und sehr kräftigen Sträuchern entwickelt haben. Sowohl die ♀- wie die ♂-Sträucher sind sehr fertil, sodass der Samenansatz ein ganz vollständiger ist. Der habituelle Typus ist für sämtliche Sträucher ein sehr ähnlicher; er ist zwischen sämtlichen Arten intermediär, jedoch mit einem Übergewicht für den *caprea*  $\times$  *viminialis*-Typus. Die Verbindung gleicht nicht wenig der Gartenart *S. dasyclados* WIMM. Ich nenne deshalb diesen in beiden Geschlechtern vorhandenen, ganz fertilen und taxonomisch sondergeprägten Typus *S. dasycladoides*. Diese Vierartverbindung ist von HÅKANSSON (1933) untersucht worden. Er hat gefunden, dass sie wahrscheinlich tetraploid ist. Da *S. viminialis*  $\times$  *caprea* haploide Gameten bildet (beide Eltern  $n = 19$ ) und *phylicifolia*  $\times$  *nigricans* eigentlich triploide ( $n = 57$ ), muss ja der Bastard  $2n = 76$ , also eine Tetraploide erhalten werden. Diese Tetraploide muss auch eine vollständige Chromosomenkonjugation haben, denn sie ist ganz fertil. Dies ist auch durch die zytologischen Untersuchungen von HÅKANSSON konstatiert worden.

HÅKANSSON zieht hieraus den Schluss, dass die Genome der vier Elternarten eine weitgehende Verwandtschaft haben müssen. Dies ist nicht ganz richtig. In der Form, wie sie sich in den sechs Zygoten der gelungenen Vierartverbindungen begegnet haben, müssen sie natür-

lich kompatibel und später konjugationsfähige Genome gebildet haben. Aber die ungeheuer überwiegende Anzahl der Einzelversuche eine Genomenverbindung zu erhalten ist ja misslungen. Die realisierten Bastarde repräsentieren daher *selektive Genomkonstitutionen*. Der Versuch zeigt also überaus klar, dass in letzter Linie *die genische Konstitution* darüber entscheidet, ob eine Genomsynthese gelingen wird oder nicht. Die Genome zweier Artbastarde können also *in der Regel inkompatibel* sein, aber *extrahierte Rekombinationsgenome* können *seltene kompatible* Verbindungen bilden. Vom genischen Gesichtspunkt ist dies ja ganz selbstverständlich, es sagt ja nichts anderes aus, als dass nur ganz extreme Kombinationen der gewaltigen Genenmasse eine durch ihren Geneninhalt konjugationsfähige Chromosomenangarnitur bilden können. Durch auxiliäre Arten können ganz unverträgliche Genome verbunden und kompatibel restituiert werden. Ein besseres Beispiel für diese Tatsache als das hier angeführte könnte kaum gefunden werden. Die Genome der *S. caprea* und *S. phyllicifolia* sind ganz inkompatibel, die der *S. phyllicifolia* und *S. viminalis* dagegen in einem Bastard vereinbar. Über *S. viminalis* gelingt also die Bildung der extrahierten Rekombinationsgenome. Der Zahl, die von den Karyologen als allzu entscheidend betrachtet wird, und die auch bei ungeraden Zahlen der Verbindung rein teilungsmechanisch eine entscheidende Rolle spielen kann (z. B. bei Triploidie), darf keine unbedingte Souveränität zugeschrieben werden. Die Konjugation der Chromosomen ist ja nicht nur ein Legespiel, sondern wird im Grunde vom genischen Inhalt der Komponenten dirigiert.

Da *S. dasycladoides* weder eine allo- noch autopolyploide Kombination ist, sondern nur die Vereinigung der Chromosomenzahlen der Elternbastarde repräsentiert ( $19 + 57$ ), so kann das sehr seltene Gelingen ihrer Synthese sowie die vollständige Fertilität des gelungenen Produkts nur dadurch erklärt werden, dass eine Gamete des Bastards *S. viminalis*  $\times$  *caprea* ein Rekombinationsgenom gebildet hat, das mit einem der drei Teilgenome der hexaploiden *S. nigricans*  $\times$  *phyllicifolia* eine konstitutionelle Verwandtschaft zeigt. Wahrscheinlich ist diese eine überwiegend *viminalis*-ähnliche Gamete gewesen, denn *S. phyllicifolia* ist ja mit *S. viminalis* kompatibel, mit *S. caprea* aber inkompatibel. Oder vielleicht war sie eine Gamete, die an gewissen *caprea*-Genen depauperiert worden war, die für die Inkompatibilität ausschlaggebend sind. Dass derartige Gene existieren, habe ich für die Kreuzung *S. cinerea*  $\times$  *caprea* zeigen können. Diese Kreuzung gelingt nur mit Schwierigkeit. Aus *S. caprea*  $\times$  *viminalis* habe ich in  $F_2$  ein





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